Investigating the role of tactile feedback during balance and walking: stimuli, neural responses, and perception

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A thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy

The University of Sheffield
Faculty of Science
School of Psychology

2024

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December 2024

Abstract

The foot soles are the primary interface between humans and the external environment, conveying information about the environment we are standing and walking upon, and contributing to balance maintenance. However, little is known about the precise role of tactile feedback in balance and gait or what feedback during such behaviours looks like. This thesis tackles this issue by first characterising pressure distributions experienced by the foot sole, investigating neural responses to forces reflective of those experienced during gait, and finally establishing a link with perception. Using pressure sensitive insoles, Chapter 2 investigates the complexity of stimuli experienced by the foot sole during everyday behaviours including standing, walking on different surfaces and at different speeds, jogging and jumping. Results revealed spatially complex foot-surface interactions, suggesting rich tactile feedback on top of the wide ranging pressures experienced. Chapter 3 utilises a combination of experimental data and computational simulations to investigate tactile responses during gait, where pressures exceed those tested in previous studies. Here, cutaneous afferents were most sensitive to dynamic stimulation, even under high forces, with slowly adapting afferent responses being highly correlated to the force applied. Finally, tactile perception at the foot sole, including under high forces, is compared to the hand in Chapter 4. The results show that interaction type (low vs high force) influences perception more than body region, but remains highly correlated across body regions. Taken together, this thesis provides new-found insight into the breadth of stimuli experienced by the foot, shining light on the under-researched spatial component of stimuli. Furthermore, the tactile system is able to continue to respond under high forces, conveying vital information regarding the contact dynamics and the

surfaces we are upon. In summary, the tactile system provides essential information during dynamic, high load behaviours that can aid in maintaining one's stability during gait.

Dedication

I am dedicating this thesis to my parents, Dave and Bernie, for their unwavering support. Over the past four years, they have listened to me talk about touch and walking for hours, and pretended to know what I was talking about. Without their motivation, and championing, I would not have grown as much scientifically, or personally. While there have been ups and downs, it was amazing to have you on board for the ride.

I must also make a special mention to Suffolk Accident Rescue Service, the East Anglian Air Ambulance, the East of England Ambulance Service, and Papworth Hospital, for ensuring that, as a family, we could share this journey following my father's cardiac arrest at the start of my PhD journey. You are all heroes!

Declaration

I confirm that the work submitted is my own, except where work that has formed part of jointly authored publications has been included. The work presented in Chapters 2 and 4 have been published, and the work presented in Chapter 3 will be published as a preprint within the first quarter of 2025. My contribution, and those of my co-authors, to this work has been explicitly indicated within each relevant chapter. I confirm that appropriate credit has been given within the thesis where reference has been made to the work of others.

Acknowledgements

I would like to start off of by sending a very special thank you to my primary supervisor, Dr. Hannes Saal. Not only did Hannes support me through my PhD, but he welcomed me into the Active Touch Laboratory during the final year of my undergraduate degree, where my research career started. Throughout my six years with Hannes, I have received phenomenal support, encouragement, and opportunities that all students can only dream of. Thank you.

Next, thank you to my two secondary supervisors: Prof. Claudia Mazzà and Dr. Jennifer Rowson. Both have provided me with essential insight into the biomechanics of gait, introducing me to a new research area, and supporting cross-department collaborations.

Thank you to all of the members of the Active Touch Laboratory, past and present, for inspiring, challenging, and facilitating insightful discussions and becoming a second family. Sharing conferences, meals, celebrations and more with you all has been a pleasure, and I cannot wait to see what the future holds for everyone!

A huge thank you to all of my collaborators for bringing essential expertise to the research presented within this thesis, with a special thanks for Dr. Toby Ellmers and Dr. Leah Bent. Toby has become a mentor, introducing me to world of balance, and Leah has become another supervisor and mentor, providing access to her lab's expertise in neurophysiology and microneurography. I will extend this thanks to Dr. Erika Howe and Ashley Vanderhaeghe, who have played an essential role in Chapter 3.

Throughout my PhD, I have had the pleasure of teaching and supervising numerous undergraduate and master's students, who have enabled me to develop in other areas of research and teaching. You have all played a key role in allowing me to get this far and have shown me that my my passion is research and I will continue in this world.

Thank you to the Discovery Medicine North Doctoral Training Partnership, funded by the Medical Research Council, for providing me with the opportunity to conduct research and complete my PhD. Similarly, thank you to the Department of Psychology for providing the further opportunities and guidance, and to the Department of Mechanical Engineering, Insigneo intistitute for *in silico* Medicine and the Neuroscience Institute, for providing the resources, space, and a home for my research

On a personal note, thank you to all of my friends, and family, for supporting me through the PhD. You may have referred to me as "the foot guy" on numerous occasions, but you have all provided me with a means to relax and enjoy life throughout my academic journey. Thank you to L'Équipe Provence for becoming a virtual cycling family, giving me an escape while we ride our real bikes, with no back wheel, indoors, to allow us to ride our virtual bikes, in a virtual world – it turns out this is also generates solutions for problems faced throughout the PhD!

A final thank you to Sam Yale. As one of my longest and closest friends, you have been there relentlessly, providing many laughs, sharing experiences, eating many pizzas and providing an alternative perspective. Thank you.

Thank you all for the memories.

Preface

The sense of touch is imperative to human interaction, not just with each other, but also how we interact with our surrounding environments, possessing discriminative and affective submodalities (McGlone et al., 2007). Touch helps us hold our favourite toys as children and communicate with our loved ones and form attachments (Hertenstein, 2002). The sense of touch allows us to feel many material properties, including temperature, wetness, roughness, and hardness. In fact, touch is powerful enough to portray emotional states without the need for visual or verbal input (Hertenstein et al., 2006).

However, while the majority of tactile research had thus far focused on the human hand, and hairy skin on the arms, tactile sensation from the sole of the is equally important. Despite this, when asking people "how do you feel the ground?", the most common answer I receive, following a pause, a look to the floor, and a confused look on their face, is "with my feet?", followed by the realisation that the foot holds great importance in everyday life.

The foot sole must able to distinguish between grass and concrete, sand and stone, and grippy and slippery, during walking so that we maintain upright, bipedal stance and do not fall. Even though humans are constantly adjusting their pressure distributions when standing, walking and running, the contribution of touch in maintaining balance is not completely understood.

Within this thesis, we will investigate the role of touch in balance from different perspectives, combining techniques from biomechanics, experimental neurophysiology, psychology and computational neuroscience, to shine a light on, and further the understanding, of the role of tactile feedback form the plantar sole during everyday behaviours.

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Chapter 1

Introduction

1.1 Introduction

Humans rely on upright, bipedal walking in every day life in order to navigate their environment, and must continually balance to prevent falls and subsequent injury. When walking, multiple sensory systems are recruited to maintain balance: the visual system, the vestibular system and the somatosensory system. The somatosensory system can be further broken down into proprioception and touch. While most research has focused on the visual, vestibular and proprioceptive systems, there has been little research specifically investigating the role of tactile feedback during balance maintenance in gait.

When considering sensory systems, there are 3 main stages of processing to consider that combine to lead to a behavioural output: input, output, and perception. An example of this can be taken from the visual system: a bright light is seen by the eye (input), leading to large responses from photoreceptors in the eye (output). This increase in firing rates leads to a large response in the visual cortex, perceived as a bright light (perception). These three steps in the processing pipeline lead to the behavioural outcome of averting gaze away from the light. When considering the involvement of the tactile feedback from the foot sole, much prior research has focused on the behavioural outcomes, looking at changes in balance and gait, following interventions designed to increase or decrease tactile feedback. To advance understanding of the role of touch, this thesis will scrutinise the role of touch during balance gait at three stages in the processing pipeline: input to the tactile system, output from the tactile system, and tactile perception during natural behaviours.

1.2 Input to the tactile system

One of the first things to consider when deciphering the contributions of a sensory system to behaviour, is the input received by the system. In the case of the tactile system at the foot sole, the inputs are the spatiotemporal pressure patterns resulting from foot-surface interaction during behaviour. There are two primary components of the pressure pattern stimuli to consider: location and magnitude. Characterisation of the magnitude of stimuli typically leads to outcome measures referring to the overall force across the entire foot, forces experienced by different regions of the foot, as well as centre of pressure (CoP). The CoP itself is a key consideration of mechanical models of balance (Caron et al., 2000), providing important information about balance stability, especially when thought of in relation to the centre of mass (CoM). Moreover, when investigating input to the systems, research has investigated the forces experienced by healthy individuals during everyday behaviour, as well as how this input changes when sensory feedback is reduced.

1.2.1 Forces experienced during everyday behaviour

Research has attempted to characterise the magnitude of stimuli experienced under unaltered sensory conditions, in healthy individuals, using pressure insoles and force plates (e.g. El Kati et al., 2010; Low and Dixon, 2010; McKay et al., 2017). McKay et al. (2017) conducted a large study on a sample of 1000 participants aged between 3 and 101 years old. Participants walked across a pressure walkway at their preferred walking speed and numerous force metrics were calculated, including peak pressure, force and contact area. Results identified that the foot experienced in excess of 600N during walking, with pressure experienced by the whole foot increasing throughout the lifespan, from 190 kPa to almost 600 kPa in males aged 3-9 and 60+ respectively. Additionally, the time the foot is in contact with the ground also increases with age, suggesting lower walking speed and a longer step cycle. Additional research had previously identified that the foot experiences up to 2000 N during jogging and jumping (Cross, 1999; El Kati et al., 2010), demonstrating that the tactile system must be able to decode a large range of forces, the magnitude of which is rarely experienced by the tactile system elsewhere on the body. Therefore, findings resulting from research elsewhere on the body should be generalised to the foot with caution.

1.2.2 Limitations of current force & pressure based studies

While current research has provided quantification of forces that the foot experiences during some behaviours, there are numerous limitations across these studies that have restricted current knowledge on the full range of stimuli that the foot sole experiences.

1.2.2.1 Tasks investigated

Although there are a range of activities that humans engage in when on foot, the two tasks that participants primarily carry out in studies investigating forces experienced by the foot sole are quiet standing and gait at self-selected speeds. While quiet standing and walking at a self-selected speed in the laboratory allow for greater control over variables, neither tasks are truly reflective of everyday behaviours. When standing in daily life, there are constant adjustments made, and rarely does one stand still for longer than a handful of seconds. Additionally, it is rare that a completely flat, smooth surface will be walked upon. Moreover, in the western world, walking barefoot is a rare occurrence outside of one's home environment. Research has already identified alterations in the way that individuals walk when first exposed to uneven terrain, with participants increasing step width and step length variability (Kent et al., 2019), placing their foot flatter on the ground (Gates et al., 2012) and reporting feeling more unsteady (Downey et al., 2022). Such alterations in the biomechanics of walking on uneven ground will be accompanied by very different input to the tactile system; instead of the typical heel-to-toe contact seen during walking on flat surfaces, surface protrusions will lead to less consistent pressure patterns, and therefore more complex tactile signals to encode. Similarly, walking on slippery surfaces alters the stimuli experienced by the foot sole. Here, an increase in pressure at the heel and toes (Fong et al., 2008) is experienced, and there is also an increased chance of experiencing shear forces, that occur both in normal gait (Tappin and Robertson, 1991) and during balance perturbations (Sutter et al., 2022). In order to understand the full complexity and nuance of the stimuli experienced by the sole of the foot during all daily activities, more challenging environments and tasks should be investigated.

1.2.2.2 Metrics investigated and reported

In studies investigating forces experienced during gait, the most common metrics reported in the literature relate to the raw pressure (in kilo Pascals) and/or force (in Newtons). While these are the most straightforward measurements to record, they are directly influenced by participant mass: the greater the mass, the greater the force. This can explain the increase in peak pressure seen by McKay et al. (2017): as age increases, so does body mass, and thus pressure. To avoid this problem and the limiting nature of using raw values, data should instead be transformed and normalized to reflect the percent of body mass experienced, allowing for the application of forces to populations with a different mass. Additionally, focusing only on the magnitude of stimuli provides little information regarding the spatial component, or detailed distribution, of the stimuli received by the tactile system.

Centre of pressure is also frequently measured due to its importance in balance and mechanical models of stability, including the inverted pendulum model (Caron et al., 2000; Gage et al., 2004; Hof et al., 2005; Winter et al., 1998). CoP itself is calculated as a weighted mean location of pressure at the foot, therefore considering the spatial component of pressure distributions to a degree. When balancing, the CoP and the CoM must stay aligned to ensure stability. Once the distance between the CoM and CoP increases, one will fall due to the reduction in stability resulting from the CoM moving outside of the base of support (Hof et al., 2005). To prevent this instability leading to a fall, one must move the body to shift the base of support with movements such as putting an arm out to balance. While knowing the centre of pressure location is important for balance, it is not currently known how much the centre of pressure informs us about the stimuli acting at the foot sole. While it is possible that cutaneous feedback can be used to calculate CoP (Morasso and Schieppati, 1999), whether or not this simple metric provides sufficient information for the tactile system to use to assist in balance, is unknown. A deeper dive into the multiple components of tactile input should be conducted to further characterise the input received.

1.2.2.3 Foot subregions

When investigating the pressure experienced by regions of the foot, it is important to also consider different parts of the foot as well as the the entire foot. This is especially important when applying our understanding of foot-surface interactions to clinical populations, such as those with diabetes, who often experience ulceration at specific foot locations, including the metatarsals which experience greatest shear forces (Caselli et al., 2002; Mueller et al., 2008). Also, considering the input in terms of multiple subregions is paramount due to the relationship between cutaneous input and muscular responses; providing additional input to regions of the foot can lead to alterations in muscular activity, (Nurse et al., 2005; Robb et al., 2021; Robb and Perry, 2022; Sharma et al., 2020; Zehr et al., 2014). Therefore, differing cutaneous input to the subregions of the foot can have effects on resulting balance control mechanisms, via the proprioceptive system. This demonstrates the need to fully characterise input to the tactile system at a local level, following segmentation of the foot into multiple subregions, rather than generally across the foot.

1.2.3 Reducing sensation

To bridge the gap between healthy and diseased populations, which experience a reduction in tactile sensation (Amaied et al., 2015; Bowden and McNulty, 2013; Deshpande et al., 2008; Kimura and Endo, 2018; Machado et al., 2016; Mizobuchi et al., 2002; Perry, 2006; Peters et al., 2016; Woodward, 1993), two primary methods have been implemented to reduce tactile sensation in healthy individuals: ice exposure and anaesthesia. Both techniques are shown to increase perception and vibration thresholds (Billot et al., 2013, 2015; D'Hondt et al., 2011; Eils et al., 2002; Ferguson et al., 2017; Fujiwara et al., 2003; Hong et al., 2007; McKeon and Hertel, 2007a,b; Meyer et al., 2004; Nurse and Nigg, 2001; Patel et al., 2011; Schlee et al., 2009b; Taylor et al., 2004a), providing the opportunity to investigate how a reduction in tactile sensation alters the input received by the tactile system at the foot sole, and the resulting behavioural consequences.

Following the reduction of sensation, walking speed reduces (Sawa et al., 2013) and contact times at the forefoot increase (Eils et al., 2002), indicating flatter foot placement is employed to improve stability in spite of the reduction in sensation. The peak pressure applied to the foot also decreases, with less pressure exerted on insensitive regions (Eils et al., 2002; Nurse and Nigg, 2001; Taylor et al., 2004a), implying that participants rely more on regions that remained sensitive to maintain balance. Further to changes in the biomechanics, changes in tactile input may impact on feedback from other systems. Reducing sensation has been shown to alter muscular responses (Aniss et al., 1992; Do et al., 1990; Peters et al., 2020; Sharma et al., 2020) to perturbations (Ferguson et al., 2017). Taken together, it is clear that a reduction in sensation leads to a myriad of changes to gait, and that these changes are not uniform across the foot. Furthermore, it is equally clear that the changes to the input received by the tactile system can change, which will have knock-on effects on balance, illustrate the multifaceted role that tactile feedback has when it comes to balance.

Focusing on biomechanical metrics, as has been the case until recently, such as peak pressure and overall contact time, restricts the ability to fully characterise tactile feedback, as the fine resolution afforded by the thousands of mechanoreceptors in the foot sole (Corniani and Saal, 2020) will be able to consider stimuli at a much finer resolution. To account for this, a more in depth quantification and characterisation of all aspects of the pressure experienced by the foot should be conducted, considering nuanced aspects of stimulation that can be decoded by cutaneous mechanoreceptors in the foot.

1.2.4 Overcoming the limitations

To overcome some of the limitations in existing research, Chapter 2 will characterise the pressure patterns experienced by the foot during everyday activities, such as standing balance, walking and jumping. As well as investigating tasks completed in typical biomechanical research, more challenging tasks will also be investigated: standing on a balance board, walking at different speeds and walking on gravel. Characterisation of the complexity of the pressure patterns during these activities in young, healthy adults will build on existing research in many ways. Firstly, the inclusion of more challenging tasks will enable the field to see how the forces that the foot experiences changes. Focusing on the spatial component of the signal, captured at a high resolution through the use of pressure sensitive insoles embedded within the shoe of the participant, will expand on current research focusing on the magnitude of the forces experienced. Secondly, beginning to consider these pressure patterns as input to the sensory system, in addition to their complexity, will pave the way towards understanding the stimuli provided to the tactile system; this is a necessary first step in understanding the contribution of tactile feedback to balance maintenance during standing and gait.

1.3 Output from the tactile system

Once the input to a sensory system has been defined and characterised, one can begin to investigate the output generated by the system that results from such input. Research investigating the output from tactile mechanoreceptors has focused on the hand, due to the key functions that the hand plays in daily life including: exploration, object grasping and manipulation, in addition to possessing a high density of receptors (Corniani and Saal, 2020). However, when walking or standing, the foot sole is the surface interacting with the external world the most, suggesting that tactile sensation from the foot deserves greater attention than it has currently been given. During standing and walking, the plantar sole must be able to decode information regarding the surface upon which one is standing, so that appropriate mechanisms can be executed to maintain balance. As previously discussed, when tactile output is reduced, differences are seen in the biomechanics of walking, including the length of time the foot is in contact with the ground (Eils et al., 2002). Additionally, alterations in the contribution from other balance control systems are also seen following a reduction in cutaneous receptor output, including proprioception where muscular activity in the lower limbs (Billot et al., 2013; Ferguson et al., 2017) and the vestibular system, where responses driven by the vestibular system are reduced (Debenham et al., 2023). However, what the output from tactile mechanoreceptors looks like during walking is unknown, and therefore the link between reduced tactile output on proprioceptive and vestibular systems remains undetermined.

1.3.1 Experimental techniques: microneurography

To investigate the responses from tactile afferents in the foot sole, research uses a technique that enables direct recordings from single afferent units, called microneurography. Microneurography is an experimental neuroscientific technique that enables recordings direct from the peripheral nerves in the legs, through which mechanoreceptor responses travel on their way to the cortex via the spinal cord. Microneurography involves the insertion of a tungsten electrode into the peripheral nerve, typically into the tibial nerve via the back of the knee, while a participant lies prone. Following the implantation of the electrode, the researcher will identify the location of the receptive field of the afferent being recorded by gently stroking the foot. The receptive field of an afferent is the area within which the afferent will respond to stimulation. Once identified, the class of the afferent is identified. There are four classes of myelinated tactile afferents in the sole of the foot, characterised by both the size of their receptive field and response patterns; fast adapting afferents respond during dynamic, but not sustained, stimulation (Knibestöl, 1973), whereas slowly adapting afferents respond during sustained indentation (Kennedy and Inglis, 2002; Knibestöl, 1975). Both fast and slowly adapting afferents can be further classified as type 1 or type 2, where type 1 afferents possess small receptive fields and type 2 afferents possesses larger receptive fields (Strzalkowski et al., 2015a; Vallbo et al., 1984). Through the implantation of an electrode directly into the nerve, it is possible to record responses from a single afferent in response to different stimulation patterns. While this technique is invasive, it affords researchers the opportunity to gather information regarding the first stage of processing within the tactile system.

1.3.2 Limitations of microneurography

While the information gathered from microneurography studies is invaluable to the understanding of tactile mechanoreceptor responses, there are limitations of this method. As the recording electrode will need to stay in place during the experiment, participants are unable to move as any movement can lead to the electrode being displaced. Even a slight contraction of the muscles around the electrode can lead to movement of the electrode. This limits the applicability of tactile responses to tasks such as walking, where there is continual movement of the foot across the ground, and standing, where there are continual micro-adjustments to maintain balance thought to activate tactile mechanoreceptors and improve feedback (Fabre et al., 2021).

The types of stimulation implemented in microneurography studies is also limited, again as a result of ensuring that the recording electrode remains static. Low amplitude-high frequency vibrations known to elicit responses from fast adapting receptors, and ramp-and-hold stimuli that elicit the characteristic responses from slowly adapting receptors to sustained indentation, are the most common stimulation types. While these stimuli are useful in identifying response characteristics and firing thresholds of afferents, the generalisability of results gained from such stimuli to the larger magnitude of forces experienced by the plantar sole during everyday behaviour is limited.

Additionally, the stimulation probe in microneurography studies often has a diameter of less than 1cm, which is part of the reason low forces are needed to generate small skin displacements. During walking and balance, the foot experiences much larger contact areas, up to 135cm^2 during walking (McKay et al., 2017; Merry et al., 2020). Therefore, the forces used in microneurography studies are not natural, but neither are the areas of contact with the stimulus. This further suggests that results from such experimental studies provide limited information regarding the tactile feedback generated during gait. Section 1.3.3 and Chapters 2 and 3 build upon the findings presented to this point by investigating the stimuli experienced during everyday behaviours in more detail, and look to combine experimental and computational methods to provide a new-found insight into tactile responses to natural stimuli.

1.3.3 Overcoming the limitations

Combining the need for highly controlled, and artificial, stimulation while the participant remains still, illustrates that the ability to extrapolate results obtained using microneurography to natural behaviours is limited. A first step to improving our understanding of tactile responses during everyday behaviour is by altering the stimuli that are presented to the foot during research when using microneurography. By applying much higher forces, that are reflective of those experienced naturally, it will be possible to broaden current knowledge on tactile responses to a larger range of stimuli. While this approach will be beneficial, stimuli presented during experimental research will still be limited to being static to ensure the electrode is not dislodged.

One avenue that can help to provide a new-found insight into tactile responses to natural and dynamic stimuli, such as the pressure patterns experienced during gait, is through the use of computational models. Recently, a computational model of tactile afferents in the foot sole, FootSim (Katic et al., 2023), was published. Using FootSim, it is possible to apply stimuli with much greater forces in simulation to investigate how tactile mechanoreceptors may provide feedback during balance and gait. Chapter 3 will extend FootSim using experimental data collected using microneurography, where both low force-high frequency, and high force-low frequency stimuli are implemented. By combining traditional experimental stimuli with new, high-force stimuli, this study will first provide insight into how tactile mechanoreceptors respond to a wide range of stimuli. Additionally, following the extension of FootSim, it will be possible to begin to characterise tactile responses to natural spatiotemporal pressure patterns, providing insights into the role that tactile feedback may play during gait.

1.4 Tactile perception

The output from the tactile mechanoreceptors in the skin of the periphery travels to the somatosensory cortex via the spinal cord for perceptual processing. Once in the cortex, sensory signals are decoded to inform us of different components of stimuli, such as shape, texture and type of stimulation (e.g. vibrations or sustained pressure). When considering the feet, we are able to identify changes in the environment that we are standing or walking on, from the carpets within our homes to gravel that we encounter during hiking. Often these surfaces include the presence of small protrusions on the surface, but equally important are smooth and slippery surfaces. Being able to detect such protrusions or slipperiness are both essential to ensure that the appropriate mechanisms are implemented to make sure upright stance is maintained, with more cautious strategies implemented (Fong et al., 2008) to counteract the reduction in perceived stability (Downey et al., 2022). Additionally, rough surfaces are thought to increase tactile feedback; this idea has been utilised by research looking to improve balance, testing the hypothesis that increasing feedback will improve balance performance.

1.4.1 Texture perception at the hand

The hand has been shown to be able to identify subtle differences in roughness gratings (Cascio and Sathian, 2001) and softness (Srinivasan and LaMotte, 1995), with no differences depending on whether participants experience passive stimulation or engage in active exploration of the stimuli (Lederman, 1981; Yoshioka et al., 2011). Different interaction mechanisms do, however, yield differing abilities to discriminate between textures, with sliding yielding a better perception of roughness than pressing (Roberts et al., 2020). At the neuronal level, responses to stimuli of differing magnitudes of roughness have demonstrated that both spatial and temporal aspects of afferent responses are required to process both coarse and fine textures (Weber et al., 2013), with different afferent classes contributing better to quantifying different perceptual dimensions (Libouton et al., 2010). FA2 (Pacinian corpuscles) afferents respond to high frequency stimulation, with their peak firing rates occurring in response to vibration frequencies between 150Hz and 200Hz (Sato, 1961). FA2 afferents are therefore able to provide information relating to skin vibrations caused by rough textures (Mackevicius et al., 2012). Surface compliance is most strongly encoded by SA1 afferents (Condon et al., 2014), and therefore, so is hardness. As balance decreases when standing on soft materials (Menant et al., 2009; Patel et al., 2011), this would suggest that SA1 afferents may be of particular importance at the foot sole, helping to encode surface hardness so that this can be perceived accurately to prevent falls. In the nerve, the speed of exploration does not alter how perception is encoded using the fingertip (Boundy-Singer et al., 2017), and neither does the contact force (Saal et al., 2018). However, the speed and forces acting at the foot during everyday behaviour are much greater than those tested in the hand, with faster walking speeds yielding greater forces (Ho et al., 2010; Taylor et al., 2004b). Therefore, in the case of the foot, the speed of interaction may yet influence perception due to the relationship with force of the interaction.

1.4.2 Limited knowledge of perception at the foot sole

While the hand has received extensive attention when it comes to texture perception, being able to sense the surface we are walking on is essential in enabling humans to adapt their strategy to maintain balance. Despite this, little is known about how the foot sole perceives different textures in the first place.

The foot experiences dramatic differences in force compared to the hand, often experiencing forces in excess of three times body mass (Cross, 1999; El Kati et al., 2010), and possesses very different skin mechanics (Lee and Hwang, 2002) and differences in mechanoreceptor densities (Corniani and Saal, 2020) compared to the hand. Research has identified that receptor thresholds at the foot sole are greater than at the hands (Kennedy and Inglis, 2002), meaning greater forces are required to activate each mechanoreceptor, and that there are differences in discrimination between foot regions (Hennig and Sterzing, 2009; Kowalzik et al., 1996). But, do these combined differences influence perception?

Many perceptual dimensions are also incredibly important during gait; it is important to understand when we are walking on a slippery surface so that an appropriate strategy can be employed to prevent falls. It is also important to understand when a surface is rough or unstable, so that we can decide to walk on a more comfortable and stable surface, and reduce our risk of falling. However, how texture perception changes at the foot compared to the hand, and how perception under forces exceeding half of a participants' body mass, as is the case in static bipedal stance, has not been investigated. Initial research has suggested that contact forces lead to altered subjective texture perception, namely increased forces resulting in textures being perceived as rougher (Lederman and Taylor, 1972; Smith et al., 2002a). Despite this, it is not known whether the forces experienced during standing or walking will alter perception further.

The few studies that have investigated perception at the foot sole have done so in terms of textural (Ofek et al., 2018) and pain (Ng et al., 2023) discrimination. Ofek et al. (2018) found that the foot is able to distinguish between different levels of roughness resulting from different types of gravel and sandpaper. Ng et al. (2023) concluded, following the application of noxious stimuli to the foot, that the foot is able to discriminate between painful stimuli better than the hand. However, research has not yet investigated perception under natural interaction conditions, such as under body weight.

1.4.3 Using texture to improve balance

Even though there is limited knowledge of how textures are perceived, textured insoles are becoming more common, with the aim of increasing tactile feedback through added texture on an insole. A benefit of using texture is the simplicity of the intervention – there is no technical engineering required to place a texture on an insole.

Morioka et al. (2009) trained participants to differentiate between different compliance levels of foam. Following 10 days of training, sway reduced when participants stood with their eyes closed, demonstrating that tactile perception could play a role in balance performance. Changing the texture of the insole of a shoe can also influence gait and balance (e.g. Aruin and Kanekar, 2013; Curuk and Aruin, 2021; Hatton et al., 2011, 2012; Kelleher et al., 2010), leading to greater load placed on the limb contralateral to the presence of the textured insole (Aruin and Kanekar, 2013). Effects have also been seen in the biomechanics of gait, where an increase in plantar flexion during walking, along with the alteration of joint moments and ground reaction forces, have been observed (Nurse et al., 2005). Improvements are greater when visual input is removed (Hatton et al., 2011), where the tactile system is leaned upon to provide a stronger input to guide behaviour. These studies all suggest that supplementing existing tactile feedback is beneficial, providing further evidence of the importance of tactile feedback to balance maintenance.

1.4.4 Addressing limited knowledge of tactile perception at the foot sole

Although the application of textured insoles has shown promise, how such textures are perceived by the foot sole has not been investigated. Chapter 4 will present a psychophysical study investigating how textures are experienced by the foot sole. This study will employ everyday textures that are experienced by the foot during everyday behaviour, such as astro turf, towels, rugs and garden decking. Textures that are used to manufacture shoe insoles will also be used, including cork and gel. Through comparisons across loading conditions (gently exploring with the foot while sat down vs full body mass when stepping onto and off of each texture) and across body parts (foot sole vs hand palm), this study will demonstrate how tactile stimuli are perceived by the foot sole. This study will then shine light on how perception differs across the body, as well as providing information about insole materials aiming at increasing tactile sensation, which may be used by manufacturers to design interventional insoles.

1.5 The role of this thesis

This thesis will investigate the role of tactile feedback during natural behaviours, such as balance and gait, using a combination of experimental and computational techniques. Each chapter will focus on one aspect of the sensory sequence outlined at the beginning of this chapter: input to the tactile system, output from the tactile system and tactile perception.

1.5.1 Chapter 2: input to the tactile system: Cleland et al. (2023)

Characterising the input to the tactile system is the first step to understanding how touch may contribute during such tasks. Chapter 2 will investigate the tactile stimuli experienced by the foot sole during both simple tasks (standing balance) and more complex tasks (walking on gravel, standing on a wobble-board).

The work presented in Chapter 2 is published in the Journal of the Royal Society Interface.

1.5.2 Chapter 3: output from the tactile system

FootSim (Katic et al., 2023), a computational model of tactile afferents at the foot sole, will be extended in Chapter 3, through the use of neurophysiological recordings of afferent responses to higher pressure loads, that mimic those experienced by the foot sole during everyday behaviour. Following the validation of FootSim, it will be possible to understand how a much broader range of pressure and pressure derivative combinations, influence firing rates of plantar sole cutaneous afferents.

1.5.3 Chapter 4: tactile perception at the foot sole: Cleland et al. (2024)

When navigating the world, we step on many different textures, including tarmac, grass and carpets. The foot experiences very different loads to the hand and it is unknown how such loads, and the lower mechanoreceptor densities and different skin mechanics, may alter texture perception. As discussed in Section 1.4.3, studies looking to improve balance and gait are beginning to use textured insoles (Aruin and Kanekar, 2013; Hatton et al., 2012; Kelleher et al., 2010; Nurse et al., 2005; Robb and Perry, 2022). Chapter 4 will investigate how different textures are perceived at the foot, and how this changes under load.

The work presented in Chapter 4 is published in the Journal of Neurophysiology.

1.5.4 Chapter 5

Finally, a discussion of the findings outlined within this thesis will be provided, considering the findings within a wider context and areas not explicitly tested in the preceding chapters. Future research topics will be proposed to better understand how tactile feedback contributes to balance and gait.

Chapter 2

Complexity of spatiotemporal plantar pressure patterns during everyday behaviours

To understand the contribution that any sensory system makes to behaviour, it is first essential to understand the input to the system. Until now, research looking at input to the tactile system during balance and gait, has focused on identifying the magnitude of the forces that the foot experiences during simple tasks, such as walking or standing still on a flat surface. Given that tactile mechanoreceptors do not respond to the overall force, which itself is rarely uniform across the foot, but must also use spatial information, such as localised pressure on the foot, more fine-grained measures of the pressures experienced are required.

During everyday behaviours, there are frequent changes in walking speed or surface texture; humans often walk on uneven pavement outside and much slower than their preferred pace when accompanied by elderly relatives. Currently, tasks investigated in research may be restrictive, and do not cover the range of stimulation that occurs naturally. Often, simple metrics such as the centre of pressure are calculated to give an indication of balance performance. While the magnitude of force, and the centre of pressure, are especially important when looking at balance from a biomechanical perspective, they only provide a limited picture of what is going on from a sensory, and, in particular, a tactile, perspective. Here, the focus will be on the spatial complexity of the signal received by cutaneous receptors, which has been shown to possess importance in tactile perception, and which is important when considering responses from a population of receptors spread across the foot.

The study presented within this chapter, published in the Journal of the Royal Society Interface, characterises the stimuli experienced by the foot during everyday life from a tactile perspective. By looking at both the magnitude of forces, in combination with the spatial component of the signal, including contact area and introducing a new metric, termed the centre of contact, the complexity of the signals experienced as input by the tactile system during everyday behaviour is analysed.

Cleland, L. D., Rowland, H. M., Mazzà, C., & Saal, H. P. (2023). Complexity of spatio-temporal plantar pressure patterns during everyday behaviours. Journal of the Royal Society Interface,

20(203), 20230052.

2.1 Author affiliations and contributions

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Within this project, I designed the protocol while focusing on tasks during which tactile feedback would be important, including more challenging tasks, which are not typically not employed in biomechanical research of gait, such as walking on gravel. Under guidance from Dr. Hannes Saal and Prof. Claudia Mazzà, the standardised protocol for each task was developed.

I led on all data collection, ensuring that the appropriate standards were met, and that all data was stored and managed in a standardised procedure. I was accompanied by Holly Rowland during data collection, to help manage to workload of multiple data collection instruments and measurements throughout the study.

Following data collection, I conducted all data management, processing, storage and analysis, under the supervision of Dr. Hannes Saal. Following analysis, I generated all visualisation, and led writing of the manuscript, along with Dr. Hannes Saal. Prof. Claudia Mazzà and Holly Rowland provided feedback and editing of the manuscript prior to journal submission, and following reviewer comments.

2.2 Abstract

The human foot sole is the primary interface with the external world during balance and walking, and also provides important tactile information on the state of contact. However, prior studies on plantar pressure have focused mostly on summary metrics such as overall force or centre of pressure under limited conditions. Here, we recorded spatiotemporal plantar pressure patterns with high spatial resolution while participants completed a wide range of daily activities, including balancing, locomotion, and jumping tasks. Contact area differed across task categories, but was only moderately correlated with the overall force experienced by the foot sole. The centre of pressure was often located outside the contact area or in locations experiencing relatively low pressure, and therefore a result of disparate contact regions spread widely across the foot. Non-negative matrix factorisation revealed low-dimensional spatial complexity that increased during interaction with unstable surfaces. Additionally, pressure patterns at the heel and metatarsals decomposed into separately located and robustly identifiable components, jointly capturing most variance in the signal. These results suggest optimal sensor placements to capture task-relevant spatial information and provide insight into how pressure varies spatially on the foot sole during a wide variety of natural behaviours.

2.3 Introduction

The foot sole acts as an interface between our body and the environment, and its placement relative to the rest of the body determines stability in balance and gait. The foot sole is also a sensory organ innervated by thousands of tactile afferents that transmit information about dynamic contact parameters to the spinal cord and the brain. Indeed, after the hands and the face, the soles of the foot are the most heavily innervated regions of the body (Corniani and Saal, 2020; Strzalkowski et al., 2018). The importance of this sensory feedback is highlighted when sensation is impaired or lost, as seen in peripheral neuropathy or via experimental interventions, leading to increased sway velocity (Meyer et al., 2004) and gait variability (Richardson et al., 2004; Wuehr et al., 2014), resulting in an increased risk of falls (Menz et al., 2006).

The nature of tactile stimuli acting on the foot sole is very different from those encountered by our hands. For example, typical forces are much higher on the foot than on the hands, and in fact the foot sole is subjected to some of the highest loads of the entire body, experiencing over 2000 Newtons during jogging and jumping (Cross, 1999; El Kati et al., 2010). Surfaces that humans typically step on are also relatively flat, while we avoid surfaces with highly uneven height profiles in order to keep the body stable and prevent injury to the foot. Finally, in contrast to the hands, most of the interactions by the foot with the environment, at least in modern times and western societies, are mediated through a shoe (Fong Yan et al., 2013), which acts as a barrier and transforms the pressure patterns acting on the foot sole (Lin et al., 2017). Together, these considerations imply a unique set of spatiotemporal pressure patterns that are typically experienced on the foot, but which are quite different from those on any other region of the body.

Previous investigations of the pressure patterns experienced on the foot sole have mostly focused on identifying differences in gait caused by various disorders and impairments, such as peripheral neuropathy. Existing research has tended to focus on static balance and normal gait (Fourchet et al., 2020; McKay et al., 2017; Merry et al., 2020; Zhang and Li, 2013). However, these activities do not cover all behaviours carried out in everyday life; we also rely on our feet during

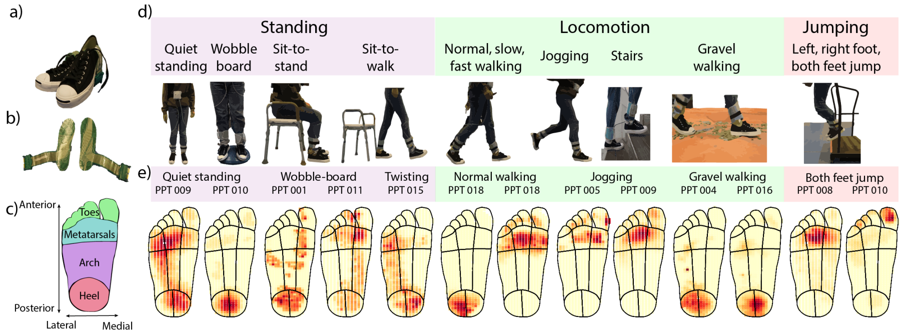

Figure 2.1: **Overview of the setup, experimental tasks, and raw data.** **a)** Standardized footwear worn by participants. **b)** TekScan®pressure insoles, recording pressure patterns with high spatial and temporal accuracy. **c)** Foot outline used for mapping, separated into the four coarse regions of the foot used during analysis. Anterior-posterior and medial-lateral axes labelled. **d)** The 15 tasks were split across three categories: standing, locomotion, and jumping. They included both stable and unstable surfaces and aimed to cover a range of everyday activities. **e)** Examples of individual frames from the pressure insole recordings.

common activities such as stair climbing, jumping, and navigating unstable or uneven ground. While existing research has been valuable for our understanding of gait, a thorough characterisation of plantar pressure patterns from a sensory perspective is important for multiple reasons. First, to understand how a sense transduces and processes information, we need to characterize the range of natural sensory experiences that this sense is exposed to. Second, when studying a sense in carefully controlled conditions in a laboratory, we want to ensure that the artificial stimuli used fall within the range of those naturally occurring. Finally, when building devices that replace or mimic the natural behaviour of the foot sole along with its sensory capabilities, for example in prosthetic applications, it is important to determine the sensing capabilities necessary for registering the full range of behaviourally relevant force patterns.

Here, our aim was to characterize the spatial properties and complexity of pressure patterns experienced on the foot sole during a range of natural everyday behaviour. We included tasks such as walking, running, jumping, and balancing, and recorded plantar pressure profiles in a young, healthy population wearing a standardized set of popular sports shoes. We analysed the locations and areas of contact on the foot sole, as well as the relationship between contact area and overall force. Finally, we quantified the complexity of spatiotemporal pressure patterns for different tasks, which yielded a small number of highly contacted independent regions whose locations suggest optimal sensor placements in future studies.

2.4 Methods

2.4.1 Participants

20 participants (3 males and 17 females) with no history of gait irregularities or foot problems provided data for this study, with mean age 19.94 (standard deviation: 2.95) years old, mean height 169.74 (10.57) cm, and mean weight 64.73 (10.13) kg. 3 participants were excluded from data analysis, because their low mass (below 50kg) prevented full calibration of the insoles. An alternative calibration was tested with one other participant, but performance was poor due to extensive signal drift with time, therefore this participant was also excluded from data analysis. All participants provided informed consent prior to the start of data collection.

2.4.2 Equipment and data collection

Participants wore the same kind of sports shoe (Converse Jack Purcell First In Class Low Top), available in UK sizes 2.5-12 (US Mens 3-12). For the current study, we used shoes between UK size 4 and 11 (modal participant size: 5). This shoe was chosen as it is commonly worn in daily life by all genders and features a relatively thin sole, which is likely to yield minimal dampening of the pressure signal.

Pressure sensitive insoles (TekScan®F-Scan®Sport Insoles, TekScan Inc., South Boston, Massachusetts, USA) were cut to each shoe size and inserted into both shoes. Each pressure sensor covered an area of 0.258 cm^2, yielding around 650 sensors for UK shoe size 4 and up to around 1050 sensors for UK shoe size 11. Each sensor was sampled at 100Hz. The recording was started and finished during each task by the participants themselves by pressing a trigger linked to the pressure insoles. The pressure insole system connected via a local network to a recording laptop, allowing the participant to move unrestricted.

Participants also wore three Opal™ wireless inertial measurement units (IMUs; APDM Wearable Technologies, Portland, Oregon, United States) throughout the experiment. Two IMUs were placed on the ventral side of both ankles and one was placed on the lumbar spine (L5). All IMUs were attached directly to the skin using double sided medical tape and secured with microporous tape. Signals from the IMUs were used during data segmentation, for example to identify when participants were walking versus turning.

2.4.3 Sensor calibration and validation

To calibrate the pressure insoles, participants first performed a step calibration protocol, provided by the TekScan research software, during which participants stood on one leg, before transitioning to the other leg. Step calibration fits the initial response of the insoles to the load applied by the participant, and also estimates and corrects for the sensor drift over time. This calibration can fail for participants with low weight, causing four participants to be excluded from the sample. Visual inspection of the live recordings in the TekScan software was used to identify any major issues in data collection. One further calibration trial was then conducted to identify the outer boundaries of the foot outline. To do this, participants were asked to roll their foot over a ball trying to cover the whole foot. Next, four validation trials were conducted to measure insole performance: 1) participants initially stood on two feet before shifting to one foot at a time and maintaining each posture for 10 seconds, 2) participants began with two feet flat on the ground, before shifting to standing on their heels and toes, each for 10 seconds, 3) participants began on two feet before shifting to the left foot and 4) participants began on two feet before shifting to the right foot. Regardless of the number of feet on the ground or posture, the total force applied during static stance should correspond to the participant's mass. The first validation trial was repeated at the start and end of the study to allow measurement of insole performance over the study. Expected participant mass during single foot standing was calculated. Based on the average calculated expected mass over a 5 second time period during the first validation trial, a constant was generated to recalibrate the pressure data during pre-processing. Following recalibration, the average participant mass during this 5 second time period would equal to the true participant mass.

Compared to standing flat on a single foot (against which the insoles were calibrated), we noted underestimation of the total force when both feet were flat on the ground by on average 10% and an overestimation when standing on a both feet by 25% during heel stance and 21% during tiptoe stance. These effects were likely due to individual sensors not reaching threshold when the overall load was spread between many sensors. Insole performance also decreased over time: the force recorded during single foot stance decreased by an average of 20%, while contact area recorded decreased by an average of 7% during the course of the experiment.

2.4.4 Experimental tasks

Participants executed up to 15 individual tasks (see Table 2.1 for list and Table S1 for full details), designed to encompass a wide range of activities that occur in daily life. These tasks belonged to one of three different categories: standing, locomotion and jumping. Three participants were unable to complete slope walking, which was conducted outside, due to adverse weather at the time.

2.4.5 Data preprocessing

All data processing and analysis was carried out in Python (version 3.8.5) using NumPy (version 1.19.1), Pandas (version 3.8.2), Scipy (version 1.5.0) and Scitkit-learn (version 1.1.1).

Table 2.1: All experimental tasks carried out by the participants, grouped by task category. Full task instructions are in Table S2.1.

Category	**Task**
Standing	Quiet standing
	Standing on a wobble board
	Sit-to-stand
	Sit-to-walk
	Standing twists
Locomotion	Normal speed
	Fast
	Slow
	Up/down a slope
	Up/down stairs
	Jogging
	Walking on gravel
Jumping	Drop jump onto both feet
	Drop jump onto the left foot
	Drop jump onto the right foot

2.4.5.1 Filtering

To filter out sensor noise, an isotropic Gaussian filter with standard deviation 0.5 (in sensor space) was applied to the spatial dimension of the data, and a Butterworth filter with a frequency cut-off of 18 Hz was applied to the temporal dimension.

2.4.5.2 Mapping the pressure data onto a standardized foot

To generate a standardized foot with optimal proportions for the cohort of participants, the length and width of participants' entire foot was measured. Then, the heel, arch, metatarsals and great toe were measured as a proportion of overall foot width and length. The length and width of each region was averaged to generate the standardized foot outline. This outline was then rotated to match the recorded pressure matrix, the position of which remained constant relative to the foot. To map the data onto the foot, the pressure matrix was scaled to match the outer boundary of the foot. First, the filtered pressure data from all tasks was concatenated. Then, the outer borders of the pressure matrix along both the anterior-posterior and medial-lateral axes were determined by identifying rows or columns in the sensor matrix that contained non-negative pressure values across any of the tasks, and empty matrix rows and columns were removed. Within the model of the foot outline, a matrix was created with a spacing corresponding to that of the sensors of the pressure insole (see Figure S2.5b). Each recorded pressure value was then mapped onto its corresponding location within the foot outline. On average, this mapping captured around 622 sensors (range: 459 to 826) and 97% of the total recorded raw pressure (see Figure S2.5d for mappings for all participants). Unmapped sensors were located close to the outline borders and yielded only small pressure values, and their exclusion is therefore unlikely to affect the overall results.

2.4.5.3 Aligning the insole and IMU data

Once recording was started for each task, participants were asked to stomp one foot, which led to easily identifiable spikes in both the pressure data and the IMU signals, which were used to synchronize both data streams. The stomp itself was deleted from the data and its time was used to signal the onset of the task.

2.4.5.4 Data trimming for standing tasks

For data analysis, data was trimmed to only include relevant aspects of each task. For quiet standing the initial 10 seconds after task onset were cut and the next 45 seconds were used in the analysis. This enabled participants to settle into a comfortable posture. 35 seconds of time stood on the wobble-board was used for analysis, beginning 10 seconds after the stomp. This was to ensure that participants were able to mount the board and find their balance. Sit-to-stand and sit-to-walk trials were designed to measure the forces during the process of getting up to a standing position. Therefore, data from sit-to-walk was analysed up until the participant began to step as identified using manual segmentation of the pressure data.

2.4.5.5 Identifying steps within the pressure data

Within all locomotion tasks, individual steps were extracted by identifying periods where the pressure signal was below a given threshold. This threshold was typically set to 500 kPa experienced across the entire foot, but was adjusted to 3000 kPa and 5000 kPa for participants 14 and 16 respectively, due to excessive contact between foot and insole when the foot was off the ground. Turns during walking were identified automatically when the gyroscope within the IMU registered a rotation of at least 45°and a turn angle of at least 115°. Manual checks and, if necessary, adjustments were made to ensure that turns were correctly identified: if any part of a step occurred while turning, as identified using the IMU placed on the lower back, or after the number of stairs climbed was completed, the step was ignored. The first and last step were removed before normalizing the length of all steps to 100 time points.

2.4.6 Data analysis

2.4.6.1 Force and contact area

Total force was calculated by summing the signals across all sensors on a given foot and expressed as a percentage of the participant's body mass. Contact area was calculated based on the proportion of active pressure sensors within the standardized foot outline. Timepoints during which total force values under 5% body mass were excluded from further analysis as these likely referred to noise caused by static contact between the insole and the foot when not on the ground. To examine differences in force and contact area between tasks within a category, Kruskall-Wallis tests were conducted, as all data violated the assumptions of normality and equality of variance. Bonferroni corrected post-hoc Mann-Whitney U tests were conducted to identify significant pairwise comparisons within task categories. To investigate the relationship between force and contact area, Spearman's Rho correlations were calculated.

2.4.6.2 Centre of pressure and centre of contact

Centre of pressure was calculated using the weighted average of all active pressure sensors. Centre of contact was calculated with each active sensor contributing an equal weight to the average.

2.4.6.3 Spatial complexity of pressure patterns

Non-negative matrix factorisation, a dimensionality reduction technique, was implemented along the spatial dimension of the data. Insole data from all participants was first scaled to a common size (UK size 11) and interpolated to fit the sensor grid for this show size, prior to mapping onto the standardized foot, ensuring that the data from all participants was of the same dimensionality: a size 11 foot with matrix dimensions of 56x20. NMF components are learned simultaneously and can therefore differ depending on how many components are extracted. To test whether the number of components affected the results, NMF models were calculated with one to thirty components, with the optimization run ten times each. Results of these simulations were consistent for each iteration, allowing for final analysis to be run once per number of components (1-30). Sensitivity analyses were conducted on a randomly selected subset of six participants and a random selection of one third of the pressure frames for each task to investigate the robustness of component locations. To identify regions on the foot which were frequently occupied by sensors with high weights in individual NMF components across tasks, we calculated pairwise correlations between all components that were required to explain 90% variance in each individual task. The resulting correlation matrix was then sorted to identify clusters by calculating the distance between component pairs using Scipy's clustering package.

2.5 Results

We recruited 20 young, healthy participants, who each executed a series of up to 15 different tasks spanning the range of everyday balancing and locomotion behaviours involving the foot sole (see Fig. 2.1d for illustrations and Methods for full details). These included balancing tasks, for example quiet standing, balancing on a wobble board, or rising from a sitting to a standing position, during which both feet were typically in contact with a surface simultaneously. We also included locomotion tasks, which comprised of walking at a number of speeds (slow, normal, fast, and jogging), up and down inclines and stairs, and on an uneven surface (gravel). In locomotion tasks typically only a single foot was on the ground at any given time. Finally, we included a number of jumping tasks, with participants instructed to jump from a low raised platform and land either on a single foot or on both feet. Participants wore a set of popular, standardized sports shoes in their size (Fig. 2.1a), which were outfitted with pressure sensitive insoles (Fig. 2.1b), capturing spatiotemporal pressure patterns with a spatial resolution of 3.9 sensors/cm^2 (average of 622 active sensors per foot across participants) at a sample rate of 100 Hz. After calibration and preprocessing, the spatial pressure data were mapped onto a standardized foot outline (Fig. 2.1c) to allow localisation of sensors and joint analysis across participants (see Methods for details and Fig. 2.1e for example frames from different tasks).

We found that the average total force experienced by a single foot (expressed as percent body mass) was in agreement with previous studies across different tasks (El Kati et al., 2010; Fourchet et al., 2020; Low and Dixon, 2010; McKay et al., 2017): just below 50% body mass for standing tasks with both feet on the ground, and 75% body mass or higher for locomotion tasks, with overall forces increasing with speed and much greater than body mass during jogging (see Figure S2.1 and Table S2.2). As expected, the highest forces were observed during jumping and jogging tasks, where loads regularly exceeded body mass more than three-fold.

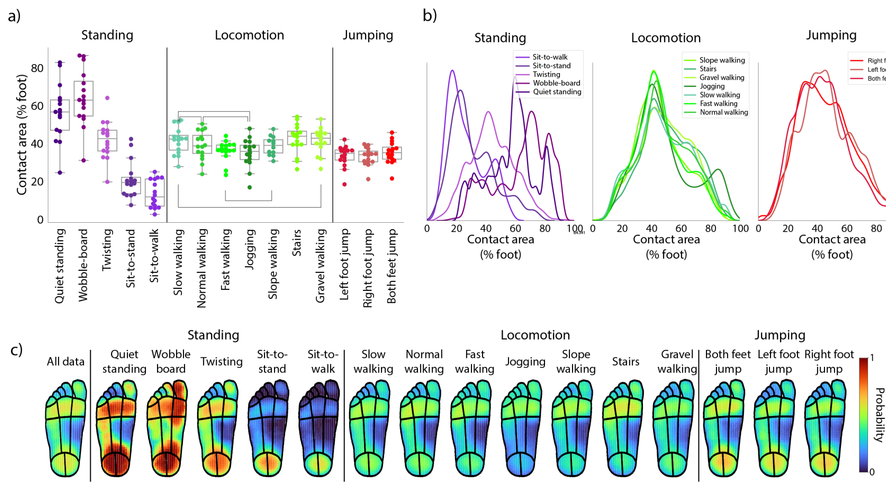

Figure 2.2: **Contact area on the foot sole across tasks. a)** Mean contact area experienced by either foot for all participants (coloured markers) across all tasks. Black horizontal lines indicate non-significant differences in Bonferroni-corrected post-hoc Mann-Whitney U tests. **b)** Distribution of contact area across individual tasks within each category. **c)** Probability of each sensor being in contact with the ground across all tasks, with red indicating high probability and blue indicating low probability.

2.5.1 Contact area

We first asked to what extent the foot sole was typically in contact with external surfaces and where on the foot sole contact was made. Because of the high spatial resolution of the pressure insoles, we were able to determine the contact area with high accuracy. During standing tasks, the average contact area experienced by the foot across all participants was around 58% of the foot, though this was highly variable both between participants (range of mean contact area of 65% when standing on the wobble board) and across the different tasks (means ranging from 27% of the foot during sit-to-walk to 64% of the foot during standing on the wobble-board. Fig. 2.2a). During locomotion tasks, the average contact area was 48% of the foot. Interestingly, mean contact area remained similar across individual tasks within this category regardless of walking speed or surface. Indeed, while Kruskall-Wallis tests conducted across tasks within a given category were all significant ($p < 0.020$, see Table S2.7), many of the post-hoc pairwise Mann-Whitney U tests in the locomotion category were non-significant, primarily including walking on flat ground in comparison to jogging and walking on gravel (see Figure 2.2a and Tables S2.8, S2.9, and S2.10).

hese findings are in direct contrast to the forces experienced in these tasks, which were highly significantly different ($p < 0.001$) within each task category (Table S2.3) as well as in all pairwise post-hoc comparisons (see Tables S2.4, S2.5, and S2.6). Contact area also varied considerably within a single task, ranging from 5% to 95% of the foot across all locomotion tasks. Comparing the distribution of contact area over time across different tasks (Fig. 2.2b) confirmed the above findings: distributions differed between standing tasks, but were remarkably consistent and almost completely overlapping across locomotion tasks, as demonstrated by almost identical mean contact areas (range: 45% to 49%) and standard deviations (17% to 20%).

Next, we quantified how often different regions of the foot made contact across the different tasks. As expected, contact probabilities were far from uniform. Overall, the heel and metatarsals were most likely to experience contact, followed by the lateral arch (see leftmost panel in Fig. 2.2c). During standing tasks, there was a clear difference between the areas of the foot likely to be in contact with the ground across individual tasks: when on the wobble-board, pressure was more likely to be spread evenly across the medial-lateral axis of the arch and the great toe was also more likely to be in contact with the ground relative to quiet standing. In the locomotion tasks, the pattern of contact areas across the foot was similar across the tasks, highlighting that the main regions involved in locomotion are the same irrespective of walking speed or surface.

2.5.2 Contact area versus force

The analysis of contact area above suggested that the extent of contact of the foot sole might often not directly reflect the overall force applied by the foot. To directly test this relationship, we correlated force and contact area and calculated the proportion of shared variance for each task classification, including all tasks within each category. There was only a moderate relationship between force and contact area ($R^2 < 0.30$ for all categories, see Fig. 2.3), suggesting that a greater area of the foot in contact with the ground does not necessarily mean a greater force experienced.

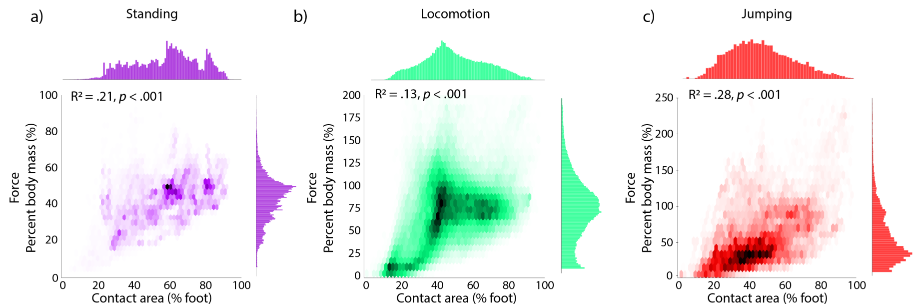

Figure 2.3: **Relationship between force and contact area on the foot sole across task categories.** 2D histograms showing relationship between overall force and contact area for **a)** standing, **b)** locomotion, and **c)** jumping categories, including data from all tasks within each category. Force and contact area exhibit a moderate positive correlation with there being a high density of data points clustered around 50% contact area and 75% body mass.

2.5.3 Centre of pressure

To maintain balance, the tactile system must consider both the magnitude and location of forces acting on the foot sole. The centre of pressure (CoP) on the foot sole is a popular measure in studies on gait and balance, mainly because of its relevance in mechanical models of balance (Caron et al., 2000). We investigated how often the CoP reflected the centre of a well-defined and relatively small contact region and how often it arose from a complex contact profile spanning larger areas of the foot. During standing tasks, the centre of pressure was primarily located at the arch (82% of time, see Fig. 2.4a), though with some variability between tasks (see example traces in Fig. 2.4c). Unlike quiet standing, CoP location was more evenly spread across the foot during locomotion and jumping (Fig. 2.4a). Contact area on the foot varied between CoP locations and was especially large for CoP locations on the arch, when on average 70% of the foot was in contact with the ground (Fig. 2.4b). During standing tasks, the CoP was within the area of contact only 62% of the time (Fig. 2.4c), reducing to as little as 40% when standing on the wobble-board (see full breakdown in Figure S2.4). Conversely, the CoP was within the area of contact 92% of the time during locomotion tasks. When in an area of contact, the average pressure at the CoP was in the 74th percentile during standing and 90th percentile during locomotion, indicating that the CoP was not necessarily located where local pressure was highest. Overall, these results highlight the fact that the CoP does not necessarily reflect the centre of single well-defined contact region but, especially during balance, is a consequence of disparate contact regions spread across the foot sole.

To further investigate how the centre of pressure relates to the overall contact region, we also calculated the centre of contact (CoC), with each active sensor having an equal weight in the calculation (see Fig. 2.4c for CoP example traces and Fig. 2.4d for CoC example traces). Differences between the CoP and CoC suggest a skewed and possibly complex, rather than a flat distribution of the pressure across the contact area. Correlating the centres of pressure and contact, we noticed that along both the medial-lateral and anterior-posterior axes, the CoP was typically located closer to the extremes of the foot than the CoC (Fig. 2.4e). For example, along the AP axis, the CoP was located more towards the heel than the CoC when considering the back half of the foot, but more towards the toes when considering the front half of the foot (Fig. 2.4f, see also examples in Fig. 2.4h).

Overall, the shared variance between the CoP and the CoC was 83% along the medial-lateral axis and 90% along the anterior-posterior axis. While this indicates a strong relationship, there were occasions when the distance between the centre of pressure and centre of contact was over 25% of the foot width and 30% of the foot length. Interestingly, there were distinct differences in how well the CoP and the CoC agreed between task categories (Fig. 2.4g), with greater shared variance along the medial-lateral axis for standing tasks, while the opposite was true for locomotion tasks. This effect can be explained by the fact that during standing a large proportion of the foot (including the heel and metatarsals) was typically in contact with the ground at any time, but pressure was focused generally at one of these locations, biasing the centre of pressure in one direction along the AP axis while the centre of contact remained central on the foot, falling in an area of no or low contact. Conversely, during locomotion typically only a small region of the foot was in contact with the ground, especially during heel strike and toe off phases of the step cycle, and therefore there was less chance for the CoP to fall far outside of a localised contact area (see examples in Fig. 2.4h). Twisting and walking on gravel were the tasks during which the greatest distance between the CoP and CoC occurred, with the distance reaching up to 30% of foot width.

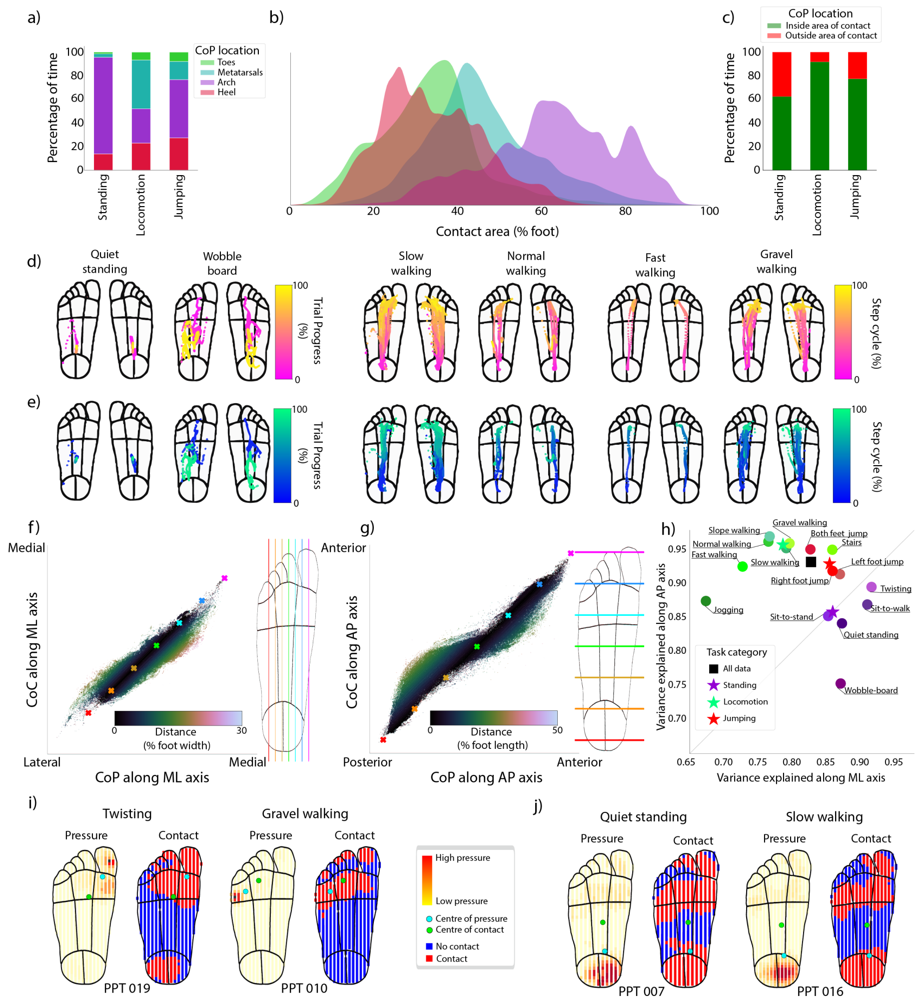

Figure 2.4: **Centre of pressure characteristics and relationship between centre of pressure and centre of contact. a)** Percentage of time spent by centre of pressure in different foot regions across task categories. **b)** Contact area when the CoP is in each of the foot regions across all tasks. **c)** Proportion of time the centre of pressure was in an area of contact for each task. **d)** Centre of pressure traces for one representative participant (PPT 004) across selected tasks. **e)** Centre of contact traces for same participant and tasks shown in c. **f)** Scatter plot showing CoP and CoC estimates along the medial-lateral axis of the foot (left). Coloured crosses indicate location along the medial-lateral axis off the foot as shown by vertical lines in the foot outline on the right. Each data point is shaded according to the distance between the CoP and CoC (see colourbar). **g)** Same as e, but for the anterior-posterior axis. **h)** Variance explained between the centre of pressure and centre of contact along the medial-lateral (horizontal) and anterior-posterior (vertical) axes across all tasks, task categories, and the whole data set. **i)** Examples of individual frames where the distance between the CoP and CoC is over 20% foot width. **j)** Examples of individual frames where the distance between the CoP and CoC is over 20% foot length.

This distance occurred due to localised pressure biasing the CoP, such as when stepping on a piece of gravel leading to a localised hotspot of pressure (Fig. 2.4h).

2.5.4 Spatial complexity

Having established that pressure is often not uniformly distributed across the contact area and that the foot sole frequently makes contact at multiple locations, we set out to characterize the complexity of the pressure patterns in more detail. To do so, we used non-negative matrix factorization (NMF), a technique that decomposes high dimensional data sets (in this case spatial distributions of pressure recorded in each sampling frame) into a small set of components that reflect uncorrelated but commonly occurring pressure patterns. The number of components needed to reconstruct the pressure distributions over time with high accuracy indicates the complexity of the pressure patterns. Moreover, the location and extent of these components on the foot sole provide insight into which regions contribute frequently and independently to overall pressure patterns and suggest locations for efficient sensor placement in future studies. We chose NMF because it is similar to other popular dimensionality reduction techniques, such as principal component analysis, but forces both the components and their respective reconstruction weights to be positive, reflecting both the bounded nature of pressure patterns as well as potential neural mechanisms (see Discussion).

For each task, we used the number of components necessary to explain at least 90% of the variance in the pressure patterns as a measure of their complexity. On average, this number was 8 across all tasks, around 100 times fewer than the average number of active sensors, demonstrating that some of their signals were highly redundant. Nevertheless, there were clear differences in complexity across the different tasks (see Fig. 2.5a, b). Balancing on a wobble-board was more complex (11 components) than flat standing (4). Sit-to-stand and sit-to-walk required the fewest number of components (4 and 3, respectively). For locomotion tasks, walking on gravel was the most complex by far (16), reflecting the higher variability and more localised pressure peaks experienced in this task. There was little difference in the complexity between walking speeds (7, 6 and 7 for slow, normal and fast walking respectively), indicating that speed does not influence spatial complexity; instead, the environment (cf. gravel) appears to be the more important factor. These differences in complexity robustly emerged across different thresholds of variance explained (minimum threshold: 65%), with gravel walking and the wobble-board consistently requiring the highest number of components.

Inspection of the individual NMF components revealed that components were generally well localised, covering only a small extent of the foot sole with typically a unimodal peak (see examples in Fig. 2.5b and the full set in Figure S2.2b), suggesting that different localised regions make independent contributions to the overall pressure distribution. Some components related to standing tasks spanned a larger proportion of the foot and were sometimes multimodal, however their regions of maximum sensitivity were generally still relatively well localised.

The first two NMF components in most tasks were located on the heel and metatarsals, demonstrating the importance of these two regions specifically, and the anterior-posterior axis more generally. During more complex tasks, such when walking on gravel, twisting, and standing on a wobble-board, components were also located in regions that barely made any contact in more simple tasks and were much more localised, indicating much more varied pressure distributions in these tasks.

Interestingly, foot regions that are often considered as single functional units were often covered by multiple distinct components with small spatial offsets and the same configuration appeared reliably across different tasks. For example, for many tasks, multiple components were located across the metatarsals: the most prominent located centrally and second one located medially. Similarly, multiple components also emerged on the heel: a primary one on the central heel, flanked by medial and lateral components on either side. Importantly, these components did not simply reflect differential placement of the foot by participants, as the spatial locations occupied by individual components remained robust when calculated on randomly selected sub-

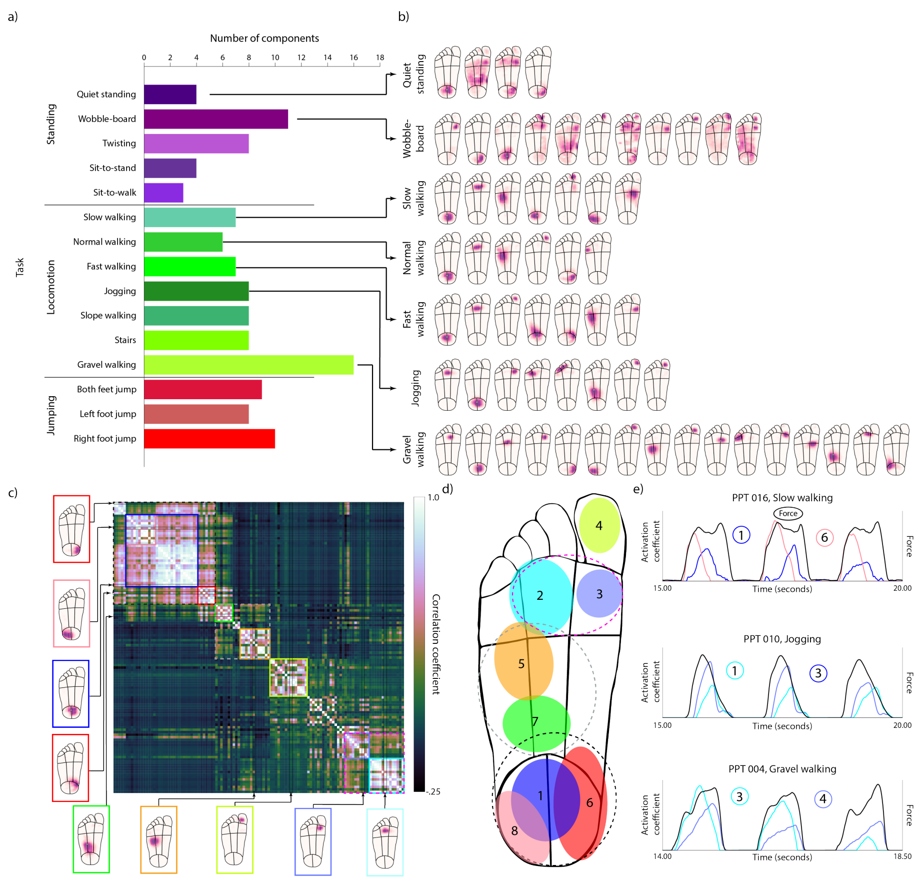

Figure 2.5: **Spatial complexity of pressure patterns on the foot sole.** **a)** Number of NMF components required to explain 90% of the variance in the spatial pressure distribution for different tasks. Many more components are required for the wobble-board and gravel walking tasks, demonstrating higher spatial complexity. **b)** Spatial plots of all components identified in panel a for selected standing and locomotion tasks, where darker shading indicates higher weight (normalized, arbitrary units). See Figure S2.2b for components from all tasks. **c)** Pairwise correlations between all components required to explain 90% in each task, sorted to display clusters containing similar components along the diagonal. Coloured boxes with solid lines indicate distinct clusters that correspond to common regions on the foot. Boxes with dashed lines indicate overarching clusters that contain multiple distinct clusters. Examples of components that feature within each cluster are shown outside of the correlation matrix with arrows pointing to their respective row/column in the matrix. **d)** General locations (shown as coloured ellipses) of distinct clusters identified from the correlation analysis (panel c). Colours for clusters are the same as in c. Numbers indicate order in which clusters emerge, with smaller numbers indicating more prominent clusters. **e)** Examples of activation coefficients over time for selected NMF components and tasks. Line colour relates to cluster location in panel d and number relates to NMF component number in panel b.

sets of the data (Fig. S2.3). Instead, the relative activation of components could signal complex interactions with the ground over time even within single participants (see Fig. 2.5e for examples showing activation coefficients over time of nearby components located in the same foot region, which demonstrate temporal offsets between components and therefore a spatial shift in the pressure distributions).

Finally, to investigate which distinct foot regions emerged robustly across different tasks, we calculated pairwise correlations between the components derived from all tasks and then ran a cluster analysis (Fig. 2.5c). Eight distinct clusters were identified from the data, each responding to a unique location on the foot: the great toe, the medial and central metatarsals, the anterior and posterior lateral arch, and the medial, central, and lateral heel (see Fig. 2.5d for an illustration). These regions emerged in a robust order when increasing the overall number of components included in the cluster analysis: first the central heel, followed by the central and medial metatarsals, indicating their big contribution to pressure patterns across virtually all tasks. Next to be identified were the great toe, anterior lateral arch and medical heel, and then finally the lateral heel and posterior arch.

In summary, analysis of spatial complexity identified robust and localised components on the foot sole that explain most of the variance in spatial pressure pattern. Unstable or uneven ground increased the spatial complexity of pressure patterns considerably. Additionally, pressure patterns are divided on the foot more finely than often considered, specifically on the metatarsals and the heel, where multiple independent sub-regions contribute separately to overall pressure patterns.

2.6 Discussion

In this study, we characterised the spatiotemporal pressure patterns that the plantar sole experiences during a range of common activities. During many of the tasks, slightly less than half of the foot sole was in contact with the ground on average. The resulting pressure distributions were not spatially uniform, but often skewed. Specifically, the centre of pressure was often biased by extreme, localised pressure. As a result, this measure, when taken alone, fails to capture subtleties in the stimuli experienced by the foot sole. Analysis of the spatial complexity of pressure signals revealed that the overall pressure distribution was well captured by a few localised components, mostly located at the heel and the metatarsals. These regions were each captured by multiple separate components, suggesting that specific, small sub-regions on the foot sole are differentially under load across different tasks and at different times.

2.6.1 Selection of everyday tasks

To understand the role of tactile feedback during posture and gait, it is essential to first understand the stimuli that are experienced by the foot sole. Existing studies investigating pressure distributions and the role of tactile feedback typically involve only simple tasks, such as walking on flat surface and quiet standing (Maurer et al., 2001; Merry et al., 2020; Stewart et al., 2007; Zhang and Li, 2013). While some research has begun to expand upon single-speed walking by investigating different speeds (Liau et al., 2021), we investigated a much broader range of tasks, including different walking speeds, surfaces and balance tasks of differing difficulty. The resulting data set allowed us to demonstrate how the distribution of pressure experienced by the foot sole of young, healthy adults differs greatly depending on the specific task, highlighting the importance of conducting a range of tasks to capture the full breadth in pressure patterns experienced during daily life.

2.6.2 Identification of relevant foot regions

A major goal of the present study was to determine which regions of the foot sole are mainly involved in contact with the ground and make relevant and separable contributions to the overall pressure patterns. Previous work has typically divided the plantar sole into three or four regions: toes, metatarsals (sometimes merged with the toes to refer to the forefoot), arch (midfoot), and heel (rearfoot) (McKay et al., 2017; Patrick and Donovan, 2018; Stewart et al., 2007). Often these mappings are inconsistent between studies, for example the rear foot can occupy up to 31% of foot length in some studies (McKay et al., 2017). When the foot sole is broken down further, there is no agreement on the number or extent of individual regions, with the arch sometimes being treated as a single region (Fernando et al., 2016; Hennig and Rosenbaum, 1991) and other times as two regions split along the medial-lateral axis (Ho et al., 2010; Merry et al., 2020). The lack of a common mapping technique between studies means limits generalisability and interpretation. Additionally, existing studies that have investigated optimal sensor placements have focused on locations that are recurrently active and allow for identification of heel strike and toe off through visual inspection (Martini et al., 2020), rather than sensors that provide information throughout a range of tasks.

Here, instead of pre-defining relevant foot regions, which can misrepresent the underlying pressure distribution (Pataky and Goulermas, 2008), we used an unsupervised method where localised and relevant regions emerged from the data itself. By choosing a wide range of natural tasks, we ensured that the resulting findings were robust across multiple different tasks, including both walking and balancing. Eight independent spatial clusters emerged from this analysis, which captured most of the information contained in the pressure patterns across all tasks: the great toe, the medial and central metatarsals, the anterior and posterior lateral arch, and the medial, central and lateral heel. Interestingly, multiple components are located within regions that are often treated as singular, specifically the heel and the metatarsals. These results indicate a more complex interaction with the ground for these regions than commonly assumed, which might have different functional roles. Overall, these results add to the emerging view that pressure distributions on the foot sole are complex and that relatively small spatial differences can be functionally and clinically meaningful (Pataky and Goulermas, 2008).

Many clinical or research applications (for example neuroprosthetic devices) require pressure sensors to be placed across the foot sole to understand how the foot has been placed on the ground. While the pressure insoles used in the current study include hundreds of individual sensors, data efficiency, device robustness, and affordability generally preclude this option and only a very limited number of sensors is viable. Our findings suggest that in order to capture the maximum amount of information across daily tasks with a minimal amount of sensors, their locations should align with the clusters identified in the present study.

Finally, while the eight identified regions capture the majority of the complexity in the spatial pressure patterns, they do not capture all of it, and this is especially true for more challenging tasks, such as walking on gravel: in these tasks, localised pressure might arise in regions on the foot not included in our set (such as on the lateral metatarsals, see component 11 for gravel walking in Figure S2.2b). It is possible that tactile feedback from these regions plays a functional role and indeed might be more relevant when tasks are difficult, so future research should study tasks that go beyond simple walking.

2.6.3 Centre of pressure

The centre of pressure is often recorded as a measure of balance, with greater path lengths and variance of the CoP taken as an indication of poorer balance. While its relevance for models of balance is undisputed (Winter, 1995), our findings indicate that it is a relatively poor proxy for the overall pressure distribution, which is often spatially complex with multiple contact regions. For example, as we have demonstrated, this metric can be biased by localised pressure when the ground is not flat, such as when walking on gravel. Additionally, the CoP is biased to the extremes of the foot, towards the toes and heels along the anterior-posterior axis, compared to the full area of contact, and this effect becomes more prominent with greater walking speed as the forces experienced at the heel and toes increase (Taylor et al., 2004b). Thus, information about pressure from regions close to the outer boundaries of the foot may be particularly relevant for the tactile system. Similarly, during quiet standing the CoP is mostly located at the arch, whereas most of the pressure signal is localised to the heel and metatarsals, while there may be little contact with the arch at all. This again suggests that any calculation of the centre of pressure by the tactile system must rely on sensory feedback from regions distant from the CoP and located towards the anterior and posterior boundaries of the foot. When the distance between CoP and CoC becomes greater, it can be identified that the environment is more complex, such as when walking on gravel. The tactile system must therefore be able to take into consideration both the location and magnitude of stimuli to keep track of the CoP in order to maintain balance and to help sense changes in the environment.

2.6.4 Implications for tactile feedback processing

Tactile feedback from the foot sole contributes important information during walking and balance, as shown by increased sway and unsteady gait when this feedback is impaired (Meyer et al., 2004; Richardson et al., 2004; Wuehr et al., 2014). However, how exactly information about contact events is represented in tactile neural responses from the foot sole or how these are processed are currently open questions. Our analysis of spatial pressure patterns identified that at most 7, and often fewer, localized NMF components could explain 90% variance in pressure profiles in all tasks, with different components active at different times and during different tasks. It is possible that the tactile system might equally rely on a handful of localized feedback components, similar to the low-dimensional common set of muscle synergies in balance and walking (Chvatal and Ting, 2013). Indeed, computer simulations have demonstrated that populations of mechanoreceptors appear to encode information via a relatively small set of spatiotemporal components (Corniani and Saal, 2020), however direct empirical evidence is currently lacking. Such feedback would also need to be integrated over large parts of the foot, for example when extracting the centre of pressure or similar measures relevant for balance. Finally, the large range of possible pressure values (from light contact to forces exceeding body weight several fold) necessitates neural mechanisms that are robust and responsive over this range. Recently, computational models have been developed that allow simulation of tactile neural responses from the foot and which will help study the nature of tactile feedback in more depth (Katic et al., 2023).

2.6.5 Limitations and future work

All participants in the current study were young, healthy adults. Pressure distributions change with age (Hennig and Rosenbaum, 1991; Machado et al., 2016; McKay et al., 2017; Price et al., 2022), disease (Fernando et al., 2016) and foot deformities (Buldt et al., 2018; Zhang and Lu, 2020). Older adults walk slower than younger adults (Menant et al., 2009; Menz et al., 2003; Wuehr et al., 2014). The elderly also shift pressure in the anterior direction towards the toes (Machado et al., 2016) away from areas that exhibit the greatest loss in tactile sensitivity, with the forefoot experiencing the greatest pressure during adulthood and older adulthood compared with adolescence (McKay et al., 2017). Similarly, in diabetic patients with peripheral neuropathy, pressure sensitivity decreases across the entire foot (Kimura and Endo, 2018) and peak pressure is greater (Bacarin et al., 2009; Mueller et al., 2008; Zhang and Li, 2013), possibly to counter the increase in pressure sensitivity threshold observed in such populations (Kimura and Endo, 2018). Changes in gait of patients with neuropathy are also exaggerated when walking on uneven surfaces (Menz et al., 2004; Richardson et al., 2004). Such alterations in gait observed in the elderly and neuropathic patients has been related to a decrease in sensitivity (Dingwell et al., 2000; Machado et al., 2016; Zhang and Li, 2013). These results demonstrate that sensitivity has a direct influence on plantar pressure experienced. The results of the current study are therefore not generalisable to populations in which changes in pressure are known to occur. Replication of the current study with older healthy and clinical populations will assist in the understanding of how tactile stimuli changes with age across a range of tasks.

The pressure patterns experienced also depend on foot shape (Mei et al., 2020; Pauk et al., 2010; Stolwijk et al., 2013), the footwear and the interaction between the two, such as the fit of the foot within the shoe (Fiedler et al., 2011), influenced by factors as simple as how tight the laces are tied. The type of shoe worn influences how one places their foot on the floor and therefore the resulting forces experienced (Charanya et al., 2004; Fourchet et al., 2020; Pezeshk et al., 2020; Stewart et al., 2007). The shoe itself, and specifically the thickness and stiffness of the sole, will also affect pressure patterns, with thicker soles spreading pressure more widely across the foot. In order to eliminate such effects in the present study, all participants wore the same brand and model of shoe. The shoe had a relatively thin sole, likely yielding more spatially fine-grained pressure patterns than might be obtained with different shoes. How exactly the shoe make affects pressure patterns will be an area of future investigation. Further research should also investigate the effects of footwear on sensory perception, which has received little interest so far (but see Schlee et al. (2009a) for an example).

While using mobile in-shoe pressure measurement systems allows for much flexibility in task design and complexity, these devices come with inherent limitations. First, pressure sensitive insoles typically record lower forces than force plates (Low and Dixon, 2010; Nakazato et al., 2011) and are harder to calibrate. Specifically, because each sensor only responds if its individual threshold is met, contact area (and pressure) will be underestimated when pressure is low and spread widely across a lot of sensors (Price et al., 2016). However, the spatial resolution afforded by insoles is much greater than force plates which allowed for in depth analysis of spatial pressure patterns on a level finer than of individual regions of the foot. In the present study, high accuracy of the measured forces was not required, as we were mainly interested in spatial patterns. Second, performance decreases during high-impact activities, such as jogging (El Kati et al., 2010). To minimise the effect of high-impact deterioration of insoles in the current study, jogging and jumping tasks were completed towards the end of the protocol and we measured insole performance both at the start and the very end of the protocol. Additionally, we restricted use of any individual insole pair to a maximum of three times before replacement. Whenever sensor dropout occurred during data collection, the pair would be replaced immediately. These actions ensured that insole performance was maintained as well as possible. Another limitation is that the insoles used in this study sampled at 100Hz, which prevents the recording of high-frequency signals. Such signals are picked up by certain classes of mechanoreceptors (Corniani and Saal, 2020; Strzalkowski et al., 2018) and are therefore likely behaviourally relevant, however they are typically of low magnitude and the current study's findings on spatial aspects of plantar pressure distributions are unlikely to be majorly affected. Finally, the insoles used in this study are capable of recording normal force only. The foot sole also experiences shear forces, particularly during the heel strike and toe off phases of the step cycle (Tappin and Robertson, 1991), and some mechanoreceptors have been found to be sensitive to skin stretch (Strzalkowski et al., 2018). Insoles capable of measuring both pressure and shear have been recently developed (Wang et al., 2022) and will be useful for future research to arrive at a more complete picture of the complex force patterns experienced during natural activities.

2.7 Data accessibility

All raw data and code used to process and analyse the data is available at *https://osf.io/n9f8w/*, DOI: 10.17605/OSF.IO/N9F8W.

2.8 Author contributions

L.D.C.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, visualization, writing—original draft, writing—review and editing; H.M.R.: data curation, methodology, project administration, writing—review and editing; C.M.: conceptualization, funding acquisition, methodology, resources, supervision, writing—review and editing; H.P.S.: conceptualization, funding acquisition, methodology, supervision, visualization, writing—original draft, writing— review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

2.9 Conflict of interest declaration

The authors declare we have no competing interests.

2.10 Funding

L.D.C. was supported by a studentship from the MRC Discovery Medicine North (DiMeN) Doctoral Training Partnership (grant no. MR/N013840/1). H.M.R. was supported by a studentship from the EPSRC Doctoral Training Partnership (grant no. EP/ T517835/1).

2.11 Acknowledgements

We would like to thank Miguel Casal for advice on the NMF analysis.

2.12 Supplementary material

Table S2.1: All tasks carried out by the participants, grouped by task category.

Category	Task	Instructions to participants
Standing	Quiet standing	Stand still, arms by your side, focusing on a point in front of you at eye-height.
	Balancing on a wobble board (35cm PhysioRoom Air Stability Wobble Cushion)	Begin off of the wobble-board, step onto the board and maintain balance. If you need, hold on to the railing during mounting, but ideally do not rely on this to maintain balance once on the board.
	Sit-to-stand	Sit with your feet at a shoulder width apart and arms rested on your thighs, then stand up.
	Sit-to-walk (4m walk)	Sit with your feet at a shoulder width apart and arms rested on your thighs, then begin walking immediately as you get up.
	Standing twists	Stand with your feet at a shoulder width apart and hands across your chest, then rotate to the left, hold, and rotate right, hold, and return to centre.
Locomotion	Self-selected speed (8m)	Walk at your normal walking speed from line A to line B and back. Repeat two times.
	As fast as possible without running (8m)	Walk as fast as you can from line A to B and back. Repeat two times.
	Slowly, as if walking with grandparents (8m)	Walk slowly, as if walking with your grandparents, from line A to line B and back. Repeat two times.
	Up/down a slope (outside, 20m, 5% gradient)	Walk at your preferred pace to the top of the slope, turn and return to start.
	Up/down stairs (14 steps, step height 16cm)	Begin with your left foot on the bottom step, walk up one step at a time. At the top turn, put your left foot on the top step, pause and descend.
	Jogging (8m)	Jog from line A to line B and back, repeat three times.
	Walking on gravel (7m walk, 20 mm gravel pieces loosely scattered)	Walk at a speed you feel safe from the start to the end of the gravel. Turn while remaining on the gravel and return. Repeat two times.
Jumping	Drop jump onto both feet (16cm drop)	Begin with both feet on the step, jump and land on both feet.
	Drop jump onto the left foot (16cm drop)	Begin with both feet on the step, jump and land on only your left foot. Once you have landed you can place the right foot down.
	Drop jump onto the right foot (16cm drop)	Begin with both feet on the step, jump and land on only your right foot. Once you have landed you can place the left foot down.

Table S2.2: Mean (SD) of pressure and contact area across tasks averaged over participants and interquartile ranges.

Task	Mean force	Force quartiles	Mean contact area	Contact area quartiles
Quiet Standing	41.49 (9.89)	33.93 48.93	55.77 (16.43)	45.32 66.55
Wobble-board	46.22 (12.45)	39.25 54.22	64.42 (18.38)	51.13 79.23
Twisting	42.35 (20.40)	29.14 52.43	44.34 (15.12)	33.88 54.65
Sit-to-stand	31.67 (18.44)	15.61 43.36	31.43 (15.30)	20.25 41.03
Sit-to-walk	29.60 (21.13)	10.53 46.20	27.02 (12.60)	16.85 36.17
Slow walking	73.50 (30.08)	59.04 91.92	48.34 (18.79)	35.17 62.82
Normal walking	82.91 (34.66)	65.97 104.33	48.17 (17.78)	36.36 61.25
Fast walking	88.83 (47.43)	54.06 119.50	45.44 (16.62)	34.30 55.95
Jogging	106.78 (71.67)	46.74 153.37	49.12 (20.11)	35.21 61.35
Slope walking	68.09 (36.42)	42.79 90.00	45.32 (16.53)	33.87 55.82
Stairs	71.42 (35.13)	50.85 90.47	50.66 (17.60)	38.17 64.30
Gravel walking	66.57 (29.21)	49.09 85.17	48.47 (17.29)	36.50 61.67
Both feet jump	49.02 (32.32)	26.87 63.01	43.38 (17.39)	30.20 54.24
Left foot jump	60.97 (50.04)	27.70 82.90	47.62 (18.45)	34.40 60.89
Right foot jump	57.92 (42.63)	28.00 80.67	45.69 (18.40)	31.29 58.08

Table S2.3: Results from Kruskall-Wallis test run on forces per task category. *indicates significance level of $p<.001$.

Task category	**Levene's test of homogeneity of variance**	**Shapiro-Wilk test of normality**	**Kruskall-Wallis H**
Standing	5585.14*	0.98*	12649.44*
Locomotion	4499.14*	0.95*	9102.16*
Jumping	280.47*	0.83*	230.26*

Table S2.4: Bonferroni corrected post-hoc Mann-Whitney U tests run on forces in each task within the standing task category. U statistic shown for each pairwise comparison. * indicates significance level of p<.008.

Task	Wobble-board	Twisting	Sit-to-stand	Sit-to-walk
Quiet standing	5246265152*	2194534021*	319399852*	118829568*
Wobble-board		1688180535*	231962102*	85485649*
Twisting			59971375*	23037320*
Sit-to-stand				2060881*

Table S2.5: Bonferroni corrected post-hoc Mann-Whitney U tests run on forces in each task within the locomotion task category. U statistic shown for each pairwise comparison. * indicates significance level of p<.002.

Task	Normal walking	Fast walking	Jogging	Slope walking	Stairs	Gravel walking
Slow walking	396224278*	207783399*	208224038*	901909057*	588264769*	667556159*
Normal walking		149063426*	144285365*	619079201*	412104661*	463332856*
Fast walking			80097946*	321478559*	213504644*	237069183*
Jogging				369395708*	249214046*	271751411*
Slope walking					498812055*	561646873*
Stairs						426380955*

Table S2.6: Bonferroni corrected post-hoc Mann-Whitney U tests run on forces in each task within the jumping task category. U statistic shown for each pairwise comparison. * indicates significance level of p<.017.

Task	Left foot jump	Right foot jump
Both feet jump	47581465*	43648768*
Left foot jump		58287796

Table S2.7: Results from Kruskall-Wallis test run on contact area per task category. * indicates significance level of p<.001.

Task category	**Levene's test of homogeneity of variance**	**Shapiro-Wilk test of normality**	**Kruskall-Wallis H**
Standing	564.15*	0.98*	37813.56.88*
Locomotion	249.03*	0.99*	1962.17*
Jumping	25.77*	0.98*	240.93*

Table S2.8: Bonferroni corrected post-hoc Mann-Whitney U tests run on contact area in each task within the standing task category. U statistic shown for each pairwise comparison. * indicates significance level of p<.008.

Task	Wobble-board	Twisting	Sit-to-stand	Sit-to-walk
Quiet standing	4954841944.5*	2950107770*	399221907.5*	156986859*
Wobble-board		2191026239*	278485944.5*	107036012*
Twisting			68137860.5*	27565498.5*
Sit-to-stand				2232182.5*

Table S2.9: Bonferroni corrected post-hoc Mann-Whitney U tests run on contact area in each task within the locomotion task category. U statistic shown for each pairwise comparison. * indicates significance level of p<.002.

Task	Normal walking	Fast walking	Jogging	Slope walking	Stairs	Gravel walking
Slow walking	480922411	275225609.5*	281561941.5	857467504.5*	500137809.5*	561420207
Normal walking		170775152.5*	174941063.5	532407301.5*	307808629.5*	345618210.5*
Fast walking			84086896.5*	255914915.5	144803053.5*	163786346.5*
Jogging				305441970.5*	178954122.5*	200041536.5*
Slope walking					445064635.5*	504008676*
Stairs						421288383*

Table S2.10: Bonferroni corrected post-hoc Mann-Whitney U tests run on contact area in each task within the jumping task category. U statistic shown for each pairwise comparison. * indicates significance level of p<.017.

Task	Left foot jump	Right foot jump
Both feet jump	46827200*	45351193.5*
Left foot jump		60974979*

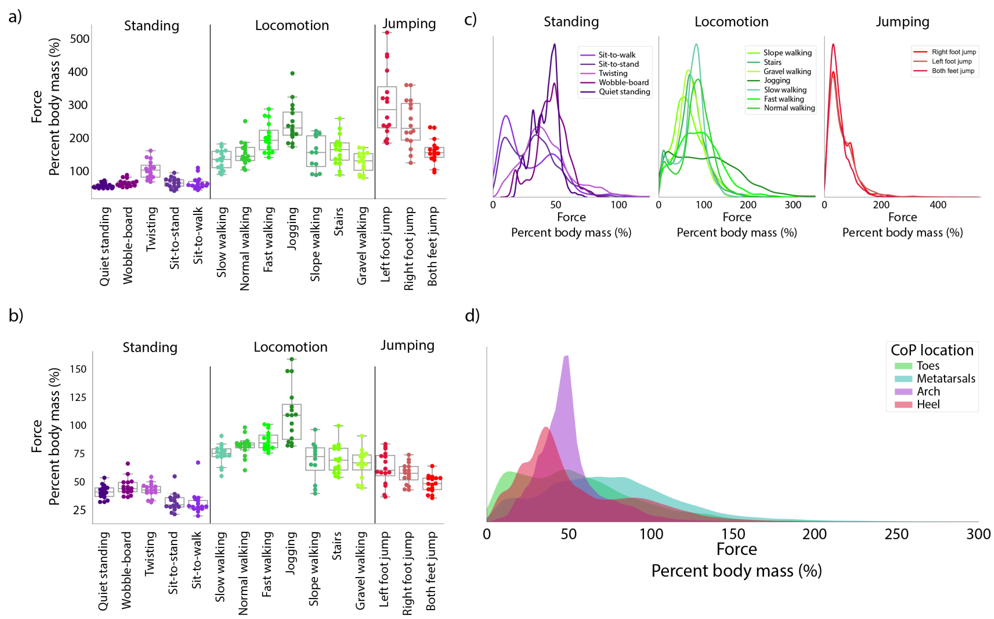

Figure S2.1: **Force experienced by the foot across different tasks. a)** Maximum force experienced by either foot for all participants (coloured markers) across all tasks. Boxplots show the distribution of maximum force over participants. **b)** Mean Force per task. **c)** Distribution of force experienced across each task within categories. **d)** Force when the CoP is in each of the foot regions across all tasks.

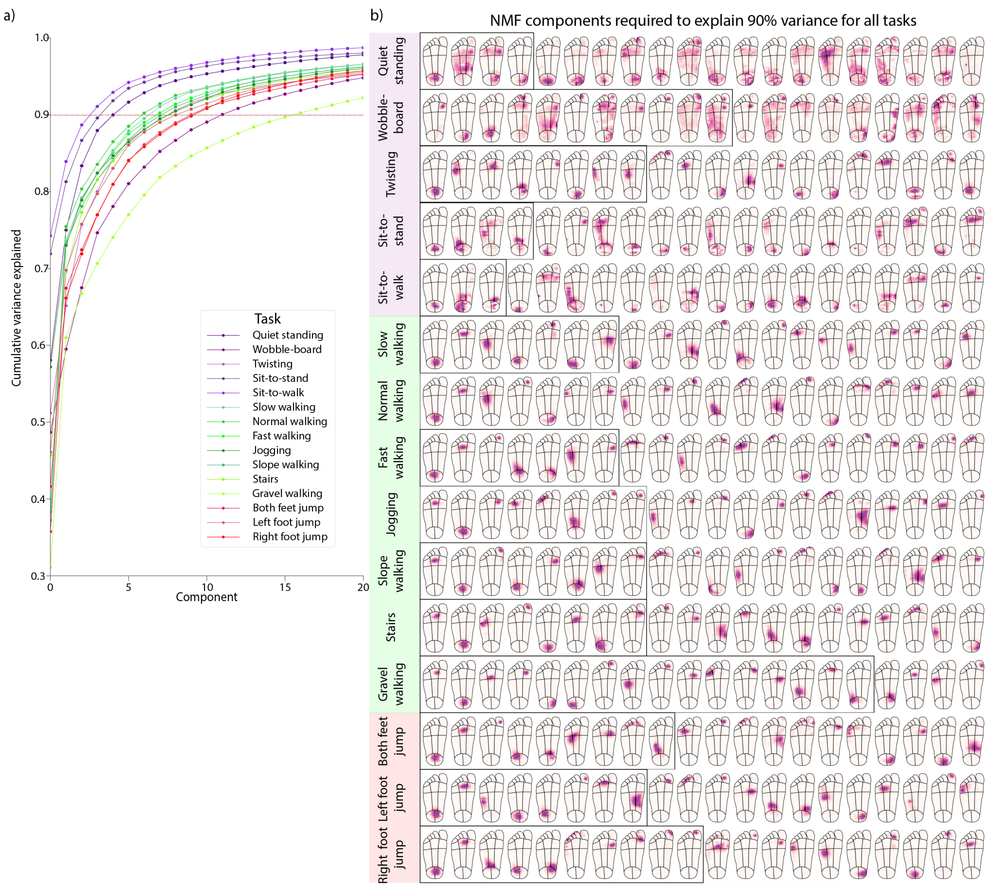

Figure S2.2: **a)** Scree plot showing variance explained by each component across tasks. **b)** The first 20 NMF components for all tasks plotted spatially on the foot. Darker purple indicates higher weight. The black box indicates the components required to explain 90% variance in the data for that tasks.

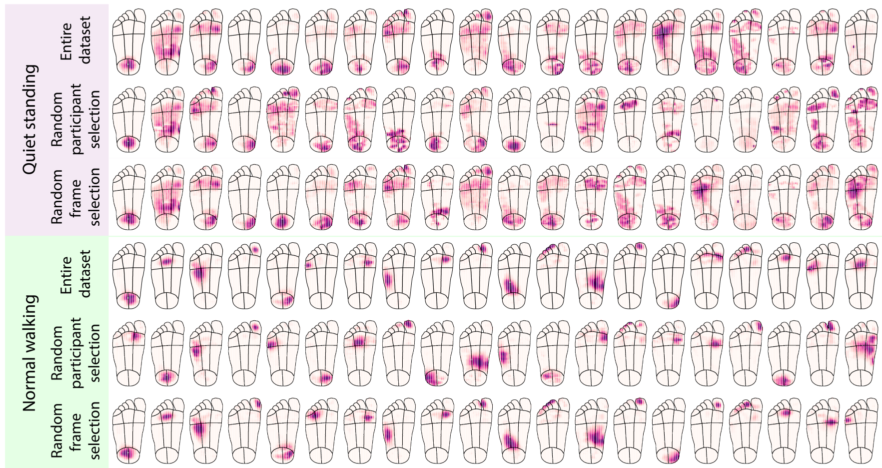

Figure S2.3: **Sensitivity analysis conducted on spatial locations of NMF components.** The first 20 NMF components for two tasks plotted spatially on the foot, calculated on the full dataset for each task, a randomly selected subset of six participants and a randomly selected subset of one third of the pressure frames for that task. Darker purple indicates higher weight. The black box indicates the components required to explain 90% variance in the data for that tasks.

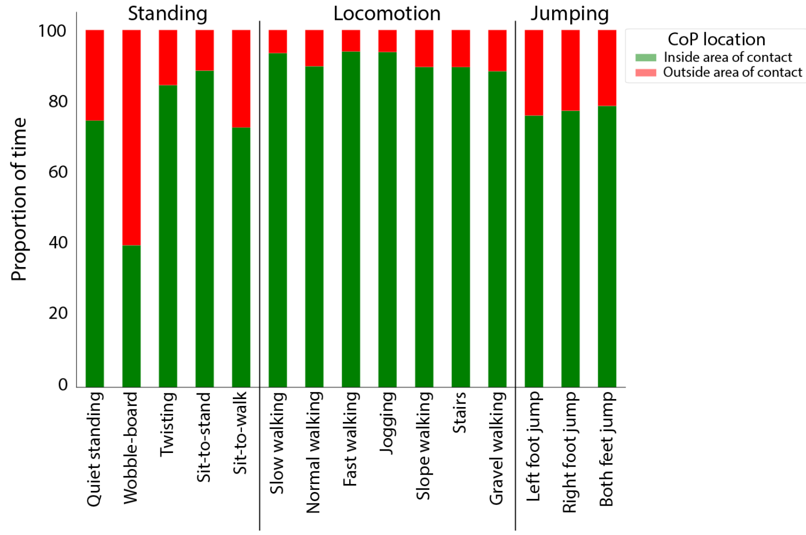

Figure S2.4: Proportion of time the centre of pressure is within an area of contact for each task.

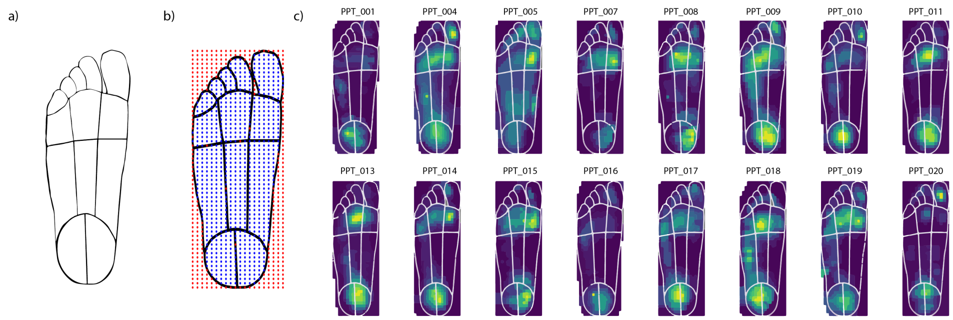

Figure S2.5: **a)** Standardized foot outline used to map the pressure data onto. **b)** Sensors mapped onto the foot outline, where blue points are sensors mapped onto the foot and red points reflect (potential) sensors not on the foot. **c)** Demonstration of how the raw pressure data aligns with the standardized foot. Mean pressure across all tasks for each participant with the standardized foot outline overlaid. Yellow indicates higher pressure, purple indicates low pressure.

Chapter 3

Plantar cutaneous afferent responses to behaviourally relevant stimuli

Chapter 2 investigated the input received by the tactile system at the foot sole during natural behaviours. The second stage of the sensory processing pipeline is output from the cutaneous receptors. Microneurography allows for direct recordings from single afferents. However, until now, research has used low-amplitude and vibratory stimuli designed to identify receptor thresholds and firing characteristics. While such stimuli are important, they fail to reflect the natural pressures that the foot experiences on a daily basis. Furthermore, studies implementing microneurography require participants to remain static due to the risks of dislodging the electrode placed onto the nerve in the back of the leg.

Computational models have the ability to overcome some of the limitations of microneurography. FootSim (Katic et al., 2023) is a computational model of tactile afferents in the foot sole, and is able to replicate the results obtained using microneurography studies to vibration stimuli. During FootSim's development, I conducted a multitude of tests to ensure that computational afferents were able to exhibit the response patterns that different afferent classes are known for, such as ensuring slowly adapting afferents would continue to respond during sustained indentation, while fast adapting afferents would only respond during the indentation and retraction phases of stimulation. I also conducted simulations of population responses during the gait cycle using spatio-temporal pressure patterns as input to the model. This generated initial ideas relating to the time-course of activity that may be present during gait. However, due to the lack of available experimental data, the magnitude of responses relating to how cutaneous afferents responded to high pressures was previously unknown.

While this chapter has not yet been submitted for publication, it will be submitted as a preprint early in 2025. The submitted version will also include simulations of population responses during gait, which are being conducted by a postgraduate student I co-supervised in 2023-24. These simulations will use computational afferents that I have developed using the data presented within this chapter.

This chapter will first characterise tactile responses to high pressure data, similar to those experienced during walking, using newly collected data. These results enhance understanding of cutaneous responses to a range of pressures. Following this, FootSim will be updated to take both low-pressure vibrations and high-pressure stimuli into account, increasing the validity of the model and its ability to replicate tactile responses to a range of stimuli.

3.1 Author affiliations and contributions

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After attending the International Society of Posture and Gait Research conference in Montréal in 2021, I was fortunate enough to spend a week with Dr. Leah Bent's neurophysiology lab at the University of Guelph, Canada. During this visit, I spent time talking with Dr. Leah Bent about how we could extend FootSim (Katic et al., 2023), including understanding of cutaneous responses under high pressure stimulation, and there the project was conceived.

Dr. Erika Howe, Dr. Nicholas Strzalkowski and Dr. Leah Bent had previously implemented ramp-and-hold stimulations using pressures reflective of those during gait. Following preprocessing of the data by Dr. Erika Howe and Ashley Vanderhaghe, the firing rates during the ramp phase and hold phase of some high pressure ramps. The processed microneurography data from eight individual afferents was forwarded to myself and Dr. Hannes Saal.

I built upon the existing model fitting code in FootSim, and extended it to include the mean firing rates during the ramp phases and hold phases of the segmented ramps. I also took a deeper dive into the processed data, which included traces typically over three minutes worth of recordings, leading this analysis and generating visualisations in Python. All of the computational replications are analysis were coded by myself.

I was the primary author of the paper in this chapter, with input from Dr. Hannes Saal, and contributions from Ashley Vanderhaeghe regarding the microneurography aspects of the methods section.

3.2 Abstract

Tactile feedback from the foot sole is important during balance and gait. However, how primary tactile neurons respond to natural stimuli to support behaviour is unknown, due to the lack of electrophysiological measurements at behaviourally relevant pressures, which much exceed those typically experienced anywhere else on the body. Here, we present naturalistic stimuli reflective of the pressures experienced during gait and record plantar cutaneous afferent responses from the human nerve using microneurography. Using this data, we extend a recently published computational model of tactile mechanoreceptors to replicate the neurophysiological response properties recorded experimentally. We find that slowly adapting neurons are only moderately sensitive to static pressure magnitude, but highly responsive to pressure changes, increasing their responses during high background pressure. Fast adapting neurons respond during both pressure onset and offset, mostly during low background pressure. While fast adapting afferents can respond to changes in stimulation following pre-loading, they do not reliably reflect the forces applied. In contrast, slowly adapting receptor response magnitudes increase during dynamic phases of stimulation. This holds true even following pre-loading, where SA receptors continue to convey information relating to the pressures experienced. The response characteristics observed are replicated using a computational model of cutaneous afferents in the foot sole, which can be used to simulate population responses to make predictions relating to how touch contributes to balance maintenance during gait. Taken together, cutaneous afferents are highly sensitive to dynamic stimulation under high pressures, such as those that occur during walking.

3.3 Introduction

Tactile feedback from the foot sole plays a crucial role in maintaining balance during standing and walking. When this feedback is removed, via cooling or anesthesia, one's ability to maintain balance deteriorates and foot placement during walking becomes more cautious (D'Hondt et al., 2011; Eils et al., 2002; McDonnell and Warden-Flood, 2000; Nurse and Nigg, 2001; Taylor et al., 2004a). Peripheral neuropathies also induce differences in foot placement and greater pressures (Mueller et al., 2008; Zhang and Li, 2013), often leading to ulceration. In contrast, increasing tactile feedback, via vibrating (Priplata et al., 2003) or textured insoles (Aruin and Kanekar, 2013), has shown to reduce sway and improve balance metrics. These and other studies have led to suggestions that tactile feedback signals parameters relevant for stability, such as the centre of pressure (Morasso and Schieppati, 1999), as well as contact locations and weight transfer during stepping (Perry et al., 2000). In addition, tactile stimuli administered to the foot during the step cycle causes both location and time dependent muscular reflexes (Aniss et al., 1992; Fallon et al., 2005; Peters et al., 2020; Sharma et al., 2020), demonstrating another role of tactile feedback and its importance in communication with the proprioceptive system.

However, the precise nature of feedback under natural conditions is unknown, hampering progress in our understanding of how tactile feedback is used. The foot sole is innervated by four classes of first-order tactile neurons, with different tuning and response properties (Kennedy and Inglis, 2002; Strzalkowski et al., 2018), whose joint signal will be more complex than a simple reflection of local pressure. Electrophysiological recordings using microneurography, a technique for recording directly from peripheral nerves, have been used to study the response patterns of individual neurons, but require the participant to be stationary, precluding recordings during natural behaviour. Additionally, the stimuli used in studies to date are low-pressure vibratory stimuli (Strzalkowski et al., 2017) or monofilaments (Kennedy and Inglis, 2002). While such stimuli are crucial for identifying thresholds and mapping receptive fields, they do not extend to the range of pressures experienced by the foot sole during everyday behaviour. Indeed, pressure

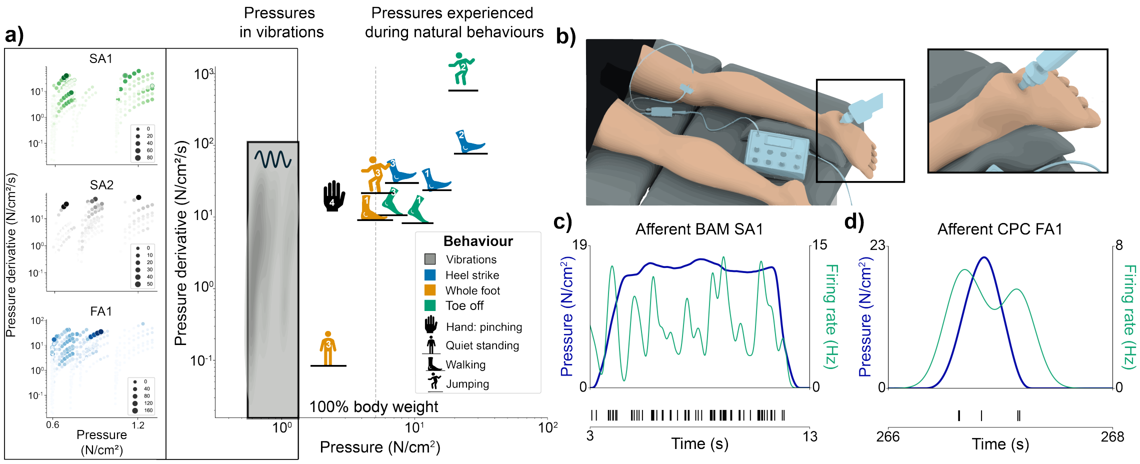

Figure 3.1: **Overview of pressures experienced during everyday behaviours and the experimental setup. a)** Pressure and derivative combinations experienced during low-amplitude vibrations employed in previous research (left, size and opacity of circles indicate firing rate) and during natural behaviour (right). 1: McKay et al. (2017), 2: El Kati et al. (2010), 3: Cleland et al. (2023), 4: Birznieks et al. (2001). **b)** Experimental setup implemented during microneurography. **c, d)** Example pressure trace and spiking response of ramp traces within experimental data collection, from one SA1 (c) and one FA1 (d) afferent.

across the foot sole during quiet standing, on the heel during initial contact while walking, and the metatarsals during push-off is at least an order of magnitude greater than those previously studied, with pressures exceeding body weight several fold (Figure 3.1a).

In order to determine the role that tactile feedback plays in balance and gait, it is therefore imperative to investigate the effects of higher pressures on afferent firing rates. This study employs microneurography to record from cutaneous mechanoreceptors during naturalistic ramp-and-hold stimuli with pressures up to 50 N/cm^2. The responses are used to extend FootSim (Katic et al., 2023), a computational model of tactile afferents in the foot sole, which can be used to conduct simulations across the entire pressure range experienced in everyday behaviours.

3.4 Methods

3.4.1 Participants

Data from six participants (mean age 23.83 years, 3 females) is included within this study. All participants had no current, or history of, neurological and circulatory disorders and reported no lower limb injuries. All participants provided written consent prior to testing. Experimental protocols received ethical approval from the University of Guelph Research Ethics Board (protocol REB#18-06-016).

3.4.2 Setup and data collection

Subjects lay prone on an adjustable massage table with the right supported using a VersaForm (Sammons Preston Rolyan, Mississauga, Ontario, CA) pillow at the ankle. Percutaneous stimulation was applied to the popliteal fossa to approximate the location of the tibial nerve (1 ms square wave pulse, 1 Hz, 0-10 mA; Grass S48, GRASS Instruments, USA) using a custom pen probe and Ag/AgCl electrodes on the patella of the right knee. A visible twitch of the plantar flexor muscles and participant reports of paresthesia indicated the correct location of the tibial nerve. The stimulation threshold was recorded as the smallest voltage output to evoke a visible muscle twitch observed in the plantar flexors.

A low-impedance reference electrode (uninsulated, tungsten 200 μm diameter; FHC, Bowdoin, ME) was inserted about 5 mm into the skin, approximately 2 cm medial to the recording site (Figure 3.1b). The recording electrode (insulated 10 MΩ, tungsten, 200 μm diameter, 1-2 μm recording tip, 60 mm length; FHC) was then inserted at the predetermined tibial nerve location.

Using mechanical stimulation, such as tapping, stroking and stretching, of the skin of the plantar foot, the recording electrode was manipulated until a single cutaneous afferent was isolated.

Neural recordings were amplified (gain 104, bandwidth 300 Hz to 10 kHz; model ISO -180; World Precision Instruments, Sarasota, FL), digitally sampled (40 kHz), and stored for analysis (CED 1401 and Spike2, version 7.2; Cambridge Electronic Design).

3.4.2.1 Neuron classification

Once a single cutaneous afferent was isolated, activation thresholds and receptive fields were identified using Semmes-Weinstein monofilaments. Activation threshold was defined as the smallest gram of force to evoke responses from the afferent 75% of the time. A monofilament with a gram force four to five times larger was then used to identify the borders of the afferent's receptive field (RF).

Afferents were classified using criteria described by Johansson et al. (1982). Units were identified as either slowly adapting (SA) or fast adapting (FA) depending on whether afferent activity persisted during a ramp-and-hold indentation within the receptive field, or whether responses were present only at the on- or off-set of contact, respectively. Units were further classified as either type 1 or type 2 based on the receptive field characteristics. Type 1 units typically have smaller receptive fields with more distinct borders, whereas Type 2 units typically have larger receptive fields with more diffuse borders.

3.4.2.2 Application of high-load stimuli

Loading was applied to the skin centred on the neuron's receptive field hotspot using a custom orthogonal loading device coupled with an in-line force transducer, a miniature button load cell (CDFM3 0-2000N, Applied Measurements, Berkshire, UK). The tip of the device was a conical frustum, with a diameter of 9 mm (Figure 3.1b). Stimulus magnitude was calculated by converting maximum pressure values experienced by the appropriate foot location during gait (Bryant et al., 1999; El Kati et al., 2010). These pressures were then normalized to the participant's body weight and then converted multiplied by the area of the stimulation probe ($0.64cm^2$), yielding a force in Newtons. This resulted in a target force, which was used to guide the ramp-and-hold stimulations. For comparisons across datasets, throughout the manuscript, we present this as a pressure, prior to the conversion to force.

The load was applied using the loading device coupled with an in-line force transducer by hand to achieve high velocities. Ramp indentations were applied at a range of approximately 3.6-163.5 $N/cm^2/s$ or with a gear crank for slower and longer duration force application (0.3- 13.7 $N/cm^2/s$). Ramp indentations were held for 3-5 seconds in duration.

3.4.3 Neural data analysis

Individual first-order tactile neurons were isolated from the neurogram using a waveform template-matching analysis in Spike2, version 7.2; Cambridge Electronic Design. Waveforms that did not match the identified unit's template were discarded. Responses were analysed across the entire experimental session to understand the responses across the range of pressures presented. Following pre-processing, data was imported into Python (version 3.12.2) using NEO (version 0.13.1). Instantaneous firing rates were calculated using the Elephant package (version 1.1.0), and smoothed with a Gaussian filter with a 150ms standard deviation.

3.4.3.1 Model fitting

Neuronal spiking models were fit to a combined dataset including the high-load data presented in the current study and data collected previously on low-pressure vibrations (Strzalkowski et al., 2017). The model architecture was identical to FootSim, a recently published model of tactile responses from the foot sole (Katic et al., 2023).

Each experimental stimulus was recreated within FootSim, placing the simulated afferent and stimulus in the same foot region as the afferent recorded from experimentally. As the high and low load datasets contained different neurons, exact matching across both datasets was not always possible. In these cases, the high-load afferent was matched as closely as possible to a vibration counterpart by identifying the foot region most similar in terms of skin hardness. The cost function used in the fitting process, defined as the error between the simulated and experimental firing rates for each stimulus, was adjusted to include the new high-pressure ramp-and-hold data:

$$cost = e_v w_v + e_r w_r + e_h w_h, \tag{3.1}$$

where e_v, e_r and e_h are the absolute difference between the experimental and simulated firing rates for vibrations, the ramp-up phase and hold phase of the ramp stimulation, respectively. w_v, w_r and w_h are the corresponding weights. During the fitting, each stimulus phase was simulated separately, following segmentation of the ramp-and-hold stimuli. The weights were chosen manually to place emphasis on the ramp and hold phases of stimulation. As the firing rates during vibrations are typically greater than those during the ramp-and-hold stimulation, e_v had the potential to be much greater than e_r and e_h. As a result, e_r and e_h had stronger weights to allow the magnitude of the error to be similar across stimuli so that the fitting process was not biased by the large responses in response to high-frequency vibrations.

FA receptors were modelled only during the dynamic loading phase, whereas SA receptor firing characteristic were examined during both the loading and plateau phases of the ramp indentation.

Models were fit using Bayesian Adaptive Direct Search in Python (PyBADS) (Ji and Ma, 2017; Singh and Acerbi, 2023). PyBADS minimized the cost function described above by making iterative choices on the optimum bounds, using existing promising solutions to guide the iterative process to identify appropriate parameters. Initially, the bounds for fitting were left loose. This enabled more freedom within the parameter space to account for the added ramp-and-hold stimuli, without restricting results to parameters known to replicate vibrational stimuli well. Following fitting iterations, visual inspection of the simulated responses for each phase of the stimuli allowed for identification of parameters that led to good responses to each stimuli. Following initial fitting, parameter bounds were tightened accordingly, and the fitting process was repeated.

Afferent model performance was compared against experimental afferent activity along multiple criteria. For slowly adapting afferents, the firing rate in response to three phases of stimuli was evaluated: vibration, ramp phase, hold phase. For fast adapting afferents, performance was assessed to two phases of stimuli: vibrations and ramp phase. An afferent model was accepted if (i) the correlation between the experimental and simulated firing rates for vibration stimuli was greater than .60, (ii) the mean simulated firing rate during the ramp period of all ramp-and-hold stimuli used was within 2 SD of the experimental firing rate and (iii) the mean simulated firing rate during the hold period of all ramp-and-hold stimuli used was within 2 SD of the experimental firing rate.

3.5 Results

To understand the responses of tactile mechanoreceptors to high pressure stimuli, we present experimental neurophysiological data collected using microneurography and combine this with computational simulations. First we analyse the neural responses to ramp-and-hold stimuli applied to multiple regions of the foot. Second, we extend FootSim to expand the range of stimuli that neural responses can be simulated in response to, while maintaining a strong performance when simulating low-pressure vibrations (Figure S3.1).

3.5.1 Response properties of first-order tactile neurons to behaviourally relevant pressures

Responses were recorded from eight tactile afferents during high pressure stimulation across six healthy participants. Figure 3.2a shows the response profiles of two slowly adapting and two fast adapting cutaneous afferents to high pressure stimulation.

3.5.1.1 Slowly adapting afferents

In line with recordings using low pressures from tactile mechanoreceptors elsewhere on the body (Iggo and Muir, 1969; Johnson, 2001), slowly adapting afferents show demonstrate sustained responses during static stimulation, and stimuli that include low rates of change (Figure 3.2a, b), maintaining their activity, albeit at a lower firing rate, during the hold phases of stimulation (Figure 3.2a, b). Slowly adapting afferents also exhibit greater responses to higher pressures compared to low pressures (see Figure 3.2a for individual examples and Figure 3.3a for the average across all slowly adapting neurons), across all rates of change in pressure; in fact, under high pressures slowly adapting afferents also respond as strongly to high rates of indentation as they do to static stimuli, as shown by hotter colours in the top half of the hexplots in Figures 3.2a and 3.3a. Computational replication of the pressure traces implemented experimentally yield computational neurons that follow the same trends observed experimentally (Figure 3.2c), with strong responses maintained throughout stimulation where there are low rates of change and to high pressures.

Next, we compared the responses of slowly adapting afferents to dynamic phases, to static phases of stimulation. The absolute firing rate experienced within the ramp phase does play a role, with faster rates of loading leading to greater firing rates across all slowly adapting afferents. Overall, the ramp-to-hold comparison revealed a consistent pattern across units: firing rates were approximately twice as high during the dynamic phase of the ramp-and-hold stimuli compared to the static phase (Figure 3.3b). We term this ratio the ‘dynamic index (DI)’, and is also mirrored computationally (Figure 3.3b). As the rates of loading investigated in this study are comparable to those experienced during gait (Figure 3.1a), this suggests that slowly adapting afferents also provide information relating to changes in pressure during natural behaviours and have .

While there is a visible preference for indentation, slowly adapting afferents also respond in-

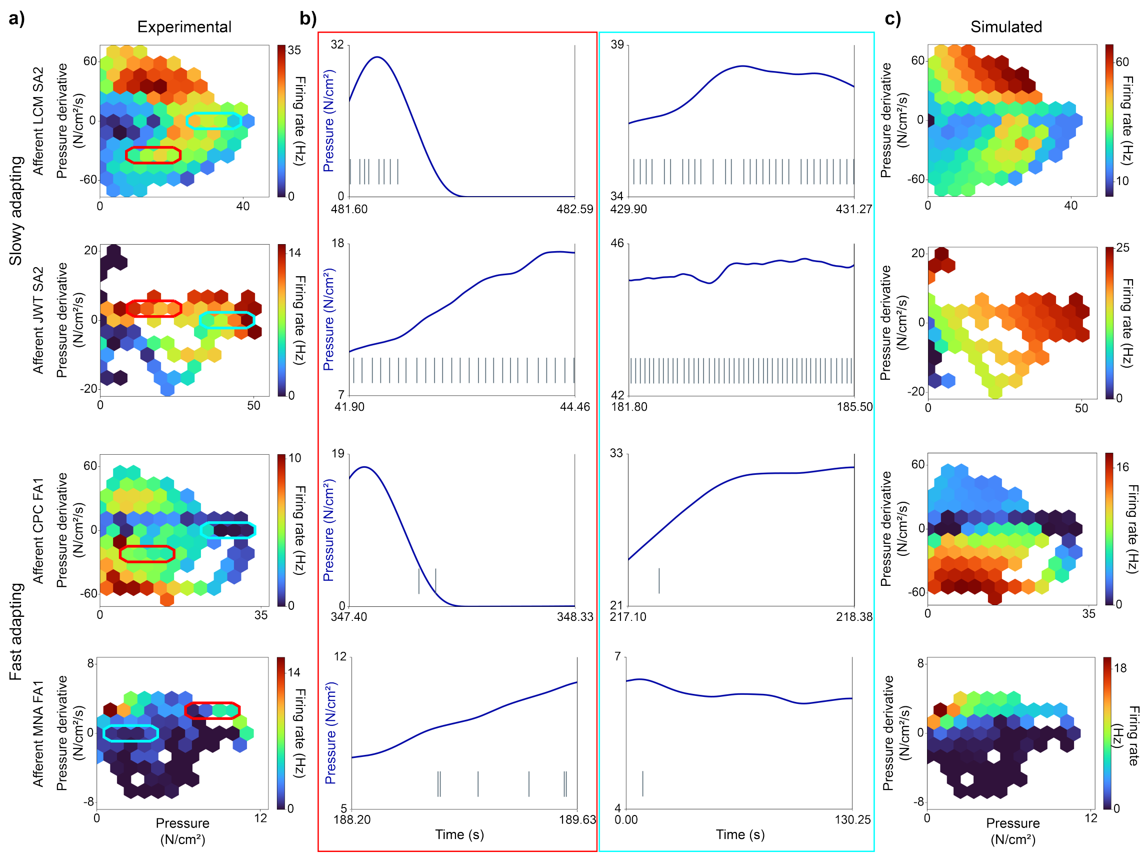

Figure 3.2: **Response characteristics of recorded and simulated afferents to high pressure stimulation.** **a)** Hexplots showing firing rates in response to pressure (horizontal axis) and pressure derivative (vertical axis; positive: indentation, negative: retraction) combinations for four individual afferents, (top) two slowly adapting and (bottom) two fast adapting. Blue colours indicate low firing rate and red colours indicate strong firing rates. White spaces denote regions of the stimulus space that were not explored. **b)** Example pressure traces (blue lines) and spiketrains (gray horizontal lines). The coloured borders match the coloured insets on the hexplots in panel a, illustrating where in the stimulus space the stimuli fall. **c)** Simulated replication of the experimental pressure trace for the same unit as in panel a, using a single computational afferent in FootSim.

creasingly to high load retractions (Figures 3.2b, 3.3c, e), although this response is of a lower magnitude than during indentations (Figure 3.3e). As this pattern exists when the rate of loading and unloading under the same pressure is similar, it demonstrates that information regarding changes in stimulation are picked up by SA mechanoreceptors and information relating to the direction of stimulation (indentation vs retraction) may be conveyed by slowly adapting afferents in the form of response magnitude.

Across both indentations and retractions and across all recorded SA afferents, responses were moderately correlated with pressure applied (r=0.54, Figure 3.3h), showing that force information may be encoded for by slowly adapting receptors. Simulated SA afferents also demonstrate positive correlations between pressure and firing rate, though on average stronger that in the experimental data (r=.85, Figure 3.3g), covering a range of correlations observed for individual afferents recorded from experimentally. Across all recorded slowly adapting afferents, firing rates typically increase beyond $5N/cm^2$, and do not continue to increase beyond $20N/cm^2$, suggesting saturation does occur at high pressures (Figure 3.3e), which has previously not been identified in slowly adapting receptors under low pressures (Knibestöl, 1975; Knibestöl and Vallbo, 1980). The same pattern of responses, increasing with force, are also accounted for by their computational counterparts in FootSim (Figure 3.3e), demonstrating the ability to respond in a way that is akin to experimental units.

3.5.1.2 Fast adapting afferents

In contrast to slowly adapting afferents, fast adapting afferents respond most strongly to dynamic stimulation, with lower firing rates exhibited when there are low rates of change in pressure, such as during the hold phase of stimulation (see Figures 3.2a, b for individual examples and Figure 3.3d for the average across all fast adapting neurons). Additionally, FA afferents demonstrate a preference for low pressure stimulation. In fact, under high pressures, fast adapting afferents do not respond as strongly to stimuli, even when there is a high rate of change (Figures

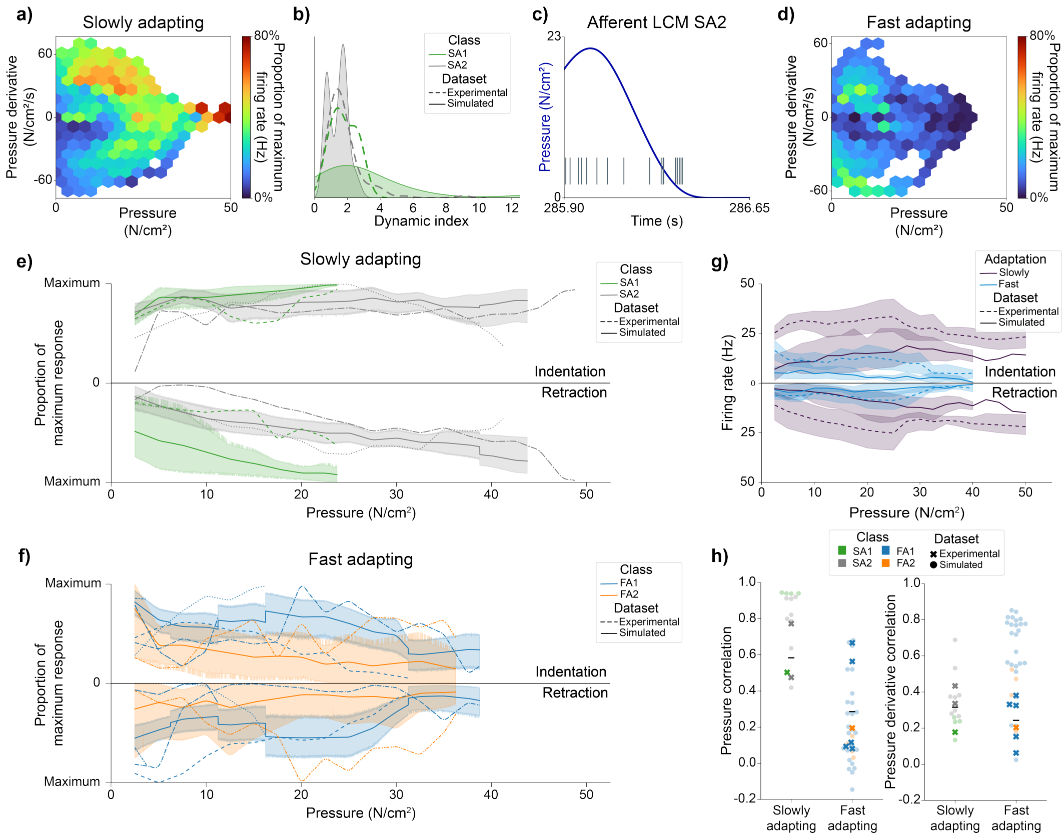

Figure 3.3: **Tuning properties of slowly and fast adapting afferents to high load stimuli. a)** Hexplots showing the average response properties across all slowly adapting afferents. Firing rates were normalised between 0 and the maximum for each individual afferent during the high load stimulations, before averaging across afferents. **b)** Kernel density plot of the 'dynamic index' of SA1 and SA2 afferents, calculated as the response during the ramp phase divided by response during the hold phase. Shaded regions indicate simulated dynamic index. Dashed lines indicate experimental data. **c)** Example of one SA2 afferent responding during a high load retraction. The blue line shows the pressure trace, and vertical gray lines reflect individual spikes. **d)** Same as panel **a** but for fast adapting afferents. **e)** Average firing rates of simulated and recorded slowly adapting neurons in response to indentation (top) and retraction (bottom) across a range of pressures, averaged across all pressure derivatives. Solid line and shaded region reflects the average across all computational afferents in FootSim. Dashed lines indicate individual afferents recorded from experimentally. Firing rates are normalized to the maximum for each simulated or recorded neuron. **f)** Same as e, but for fast adapting neurons. **g)** Lineplot showing the magnitude of responses to the range of pressures implemented. The solid line indicates the mean across all computational afferents. The dashed line indicates the mean across all experimental afferents. **h)** Correlation coefficients of the relationship between pressure and firing rate (left) and between pressure derivative and firing rate (right). Solid crosses indicate coefficients calculated from experimental afferents, and shaded circles indicate correlation coefficients calculated using computational afferents.

3.2a and 3.3d), suggesting that fast adapting receptors become less sensitive to the magnitude of change when already loaded with high pressures.

FA responses tend to not increase, and on average they decrease, beyond $5N/cm^2$ (Figures 3.2f, 3.3f). Across all units, fast adapting receptors showed a lower magnitude of responses to all pressure ranges in comparison to slowly adapting receptors. On average, fast adapting receptors responded with firing rates 5.0 times lower than slowly adapting receptors (5.9 times lower when considering indentations and 4.2 when considering retractions, Figure 3.3g), indicating that FA receptors provide limited information about stimuli in this pressure range, despite high rates of change. These differences in the magnitudes of responses of cutaneous mechanoreceptors to high pressure stimuli are replicated using FootSim (Figure 3.3g), where slowly adapting receptors exhibit stronger responses to high pressure stimulation than fast adapting receptors.

While FA receptors do increase firing up until approximately $5N/cm^2$, there is a weak correlation between pressure applied to the foot sole and mean firing rate in response (average r=.18, Figure 3.3h). This saturation supports the notion that FAs are much less sensitive under high pressures. Computational replication of the experimental protocol shows that FootSim's fast adapting afferents respond with a similar average correlation between force and response (r=.09), with computational afferents also covering the same range of correlations seen experimentally (Figure 3.3h).

3.5.2 Loading beyond 100% body weight

During everyday behaviour, the foot is rarely loaded from zero, but instead the foot is already often loaded before we initiate movement, such as beginning to walk from a standing start. To investigate how cutaneous receptors respond to stimuli following being loaded, we pre-loaded afferents to 100% body weight, before holding this pressure for 4-5 seconds. Following this, pressure was increased up to approximately 125% body weight before retracting back to the body weight

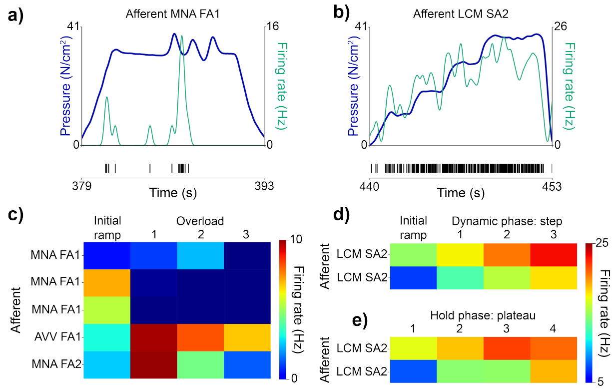

Figure 3.4: **Mechanoreceptor responses following preloading.** **a)** An example of the overloading protocol from a single fast adapting afferent, and the spiketrain recorded during the procedure. **b)** An example of the step-loading protocol from a single slowly adapting afferent, and the spiketrain recorded during the procedure. **c)** Heatmap to show the responses during the overloading procedure. Hot colours indicate a stronger response. Afferents show sensitivity but but a consistent response strengths across overloads. **d, e)** Heatmap to show the responses during the dynamic (d) and static (e) phases of the step-loading procedure. Hot colours indicate a stronger response. Responses increase consistently within the dynamic phases but less consistently in the plateau phases.

baseline for three times (Figure 3.4a). This process was repeated for three fast adapting units; one of the fast adapting afferents had three iterations of this process applied, one early in the recording and two towards the end, totalling five overloading processing in FA units.

Each overload application involved mean rates of loading similar to the initial ramp (mean during the initial ramp: 6.9N/cm^2 and mean during the three overloads: 6.8$N/cm^2/s$, 5.1$N/cm^2/s$ and 6.8$N/cm^2/s$ respectively, Figure 3.4a), and therefore only differed in whether pre-loading was applied to the plantar sole. Despite being pre-loaded, in four of the six presentations across afferents, the afferent was still sensitive to the overloading stimulation, although the responses were not consistent across repetitions (Figure 3.4c). In three of these procedures, the firing rate during the first overload was higher than that recorded during the initial ramp, demonstrating that despite holding a preload, cutaneous afferents are still sensitive to changes in stimulation. However, the reduction in firing rate seen between overloading applications demonstrates that this sensitivity reduces if repeated changes occur in quick succession; here, the three overloads were applied within 4 seconds, with each ramp up lasting approximately 250 ms. This reduction across overloads, despite the same pressures being applied, suggests that the magnitude of both the pressure, and rate of change in pressure applied, is not conveyed reliably by tactile afferents, leaving information only that a change has occurred being transmitted.

In a similar procedure, one SA2 afferent was loaded in steps (Figure 3.4b) on two occasions. Here, the unit was loaded to approximately $12N/cm^2$, $22N/cm^2$, $31N/cm^2$ and $39N/cm^2$ at rates of loading averaging $4.0N/cm^2/s$, $3.6N/cm^2/s$, $2.3N/cm^2/s$ and $3.4N/cm^2/s$ respectively for each step, and held for 0.5s after each ramp. During the dynamic phase of the stimuli, the firing rate increased with the addition of increasing pressure (Figure 3.4c), with a greater firing rate in response to the higher loads applied, despite similar pressure derivatives being applied. Firing rates during the hold phases did also increase, although less reliably than during the dynamic aspects of the stimulation, with the firing rates between some hold periods not increasing despite increased load (Figure 3.4d).

Responses following pre-loading suggest that the majority of tactile feedback will occur where changes are occurring. Slowly adapting receptors appear to provide information regarding the magnitude of the pressures experienced, while fast adapting receptors show that there is a presence of change, but do not convey information relating to magnitudes after being loaded to a degree where they are no longer as sensitive.

3.6 Discussion

In the current study, we investigated the responses of plantar sole cutaneous afferents to pressures reflective of those experienced during gait. Microneurography recordings showed that slowly adapting afferents respond more favourably to high pressures than fast adapting afferents, also preferring indentation to retraction. Afferents are differentially sensitive to the magnitude of pressures, and the magnitude of the pressure changes, beyond 10 N/cm^2: fast adapting afferents appear to provide little information above this pressure, whereas slowly adapting afferents are less sensitive to the magnitude of pressure during static stimulation. However, tactile mechanoreceptors are still sensitive to the presence of a change, even if they are pre-loaded, as would be the case when initiating gait from a standing start.

3.6.1 Cutaneous feedback during sway

When standing, humans do not remain perfectly still, but instead execute continuous adjustments in posture to remain stable, visible through fluctuations in the centre of pressure (Panzer et al., 1995). Prior research has suggested that that these these adjustments in pressure distribution occur in an attempt to reactivate mechanoreceptors (Fabre et al., 2021). The results from the overloading and step-loading procedures provide further evidence supporting the importance of sway in increasing tactile feedback, showing sensitivity of cutaneous afferents to the presence of changes in pressure. As both fast and slowly adapting afferents are sensitive to these changes suggests that, despite FA receptors preferring high frequency stimulation and changes in stimuli (Knibestöl, 1973), slowly adapting receptors may contribute with equal importance to balance.

Due to the reduced responses, and reduced specificity of responses during sustained pressure, it is likely that there will be limited information provided by cutaneous mechanoreceptors at the current location of pressure at the foot. However, as soon as movement is initiated, such as during sway when standing to the beginning of gait, tactile feedback will increase: fast adapting receptor will signal the presence of a change in pressure, complemented by slowly adapting afferents providing information relating to the magnitude of the pressures applied. This notion posits that tactile feedback is most important during dynamic behaviours.

3.6.2 Skin mechanics

Tactile mechanoreceptors are activated as a direct result of changes in skin displacement. The relationship between pressure and skin displacement is non-linear and increases beyond 10mm at pressures over $20N/cm^2$ (Vanderhaeghe et al., 2024; Xiong et al., 2010). This nonlinearity arises from an increase in skin stiffness under higher pressure (Pailler-Mattei et al., 2008), resulting in a less of a change in indentation for equivalent force increases under high load. Given that slowly adapting afferents respond more strongly to high pressure stimulation, where changes in skin indentation are much reduced, stimuli at higher loads also meet the preference of SA afferents to low-derivative and more static stimulation. As the pressures increase, the change in skin indentation will decrease, therefore the saturation in pressures seen may be due to the similar levels in skin indentation. Similarly, this nonlinearity may contribute to fast adapting afferents preferring low pressure stimulation, where the change in skin indentation with increasing pressure is much greater below $5N/cm^2$.

The viscoelastic nature of skin means that the skin does not rebound back to it's resting position immediately after stimulation has stopped. In fact, this deformation has been shown to activate SA2 afferents (Saal et al., 2023), and may contribute to some responses seen during retractions of the stimulus. As the skin may remain heavily displaced, skin stretch could persist longer than the stimulation probe is in contact with the skin or retract at a slower rate than the manual retractions used in the study. As a result, slowly adapting receptors may continue to spike as the skin profile may not directly reflect the stimulation profile. This information may useful by providing information regarding the amount of pressure that was applied, such as when the heel becomes unweighted following heel strike in the gait cycle.

While high pressure leads to high levels of skin displacement, it is important to note that the effects of such stimulation will also lead to waves that propagate across the skin, which could travel many centimeters (Manfredi et al., 2012). Under such high levels of indentation, receptive fields of mechanoreceptors are also much greater (Johansson, 1978), meaning that stimulation in one location may activate receptors centimeters away. These ripples act as high frequency, low amplitude vibrations, which may occur where mechanoreceptors are not already loaded, can activate fast adapting, and particularly FA2, receptors elsewhere on the foot, due to their strong responsiveness to vibrations (Manfredi et al., 2012). As the skin on the foot is harder than at the hands (Falanga and Bucalo, 1993; Strzalkowski et al., 2015b), it is possible that these signals may propagate faster and further than has been measured previously. If this does happen, then it is possible that fast adapting receptors may contribute to balance maintenance as a result of remote stimulation, in addition to the strong SA responses identified within this study.

3.6.3 Shear

Here, we applied high pressures to the foot sole which resulted in skin displacements exceeding 10mm (Vanderhaeghe et al., 2024; Xiong et al., 2010). Such large displacements of the skin, in combination with some pressures applied tangentially resulting from handheld stimulation generating shear, will lead to elevated levels of skin stretch and shear. Shear stimulation has been shown to activate SA2 (Johansson, 1978; Johansson and Vallbo, 1983) and FA1 (Delhaye et al., 2021; Johnson et al., 2000) receptors preferentially. It is therefore likely that these pressures contributed to the strong responses of SA2s to high pressure stimulation.

While the contribution of shear has not been disentangled here, the overall response characteristics of slowly adapting receptors are successfully replicated computationally using FootSim (Katic et al., 2023). Computationally, currently, this information is encoded implicitly within FootSim, allowing the model to maintain its simple skin mechanics model. However, the 3D geometry of the foot, and non-normal means that truly natural stimulation multifaceted, including dynamic changes in the directions that forces are acting at the skin. Thus, while the results in the current study provide the first look at cutaneous responses to high loads, further systematic investigations should be conducted to investigate responses to stimulation from angles reflecting heel strike and toe off, along with controlled shear application.

3.6.4 Population responses

This study has provided new information regarding the response properties of cutaneous afferents at the foot sole to pressures comparable to those experienced in gait. We have presented experimental recordings from single afferents, which have enabled multiple computational equivalents to be generated. Using computational afferents within FootSim, it is possible to generate afferent populations, with population densities in line with predictions made in the literature (Corniani and Saal, 2020; Strzalkowski et al., 2018). Conducting simulations using these populations will provide powerful insight into tactile feedback during gait, and how this relates to dynamic stimulation. Additional, computational models can provide new insights that are difficult to identify neurophysiologically due to the limitations of microneurography, where, currently, only single afferents can be recorded from at a time, and in response to unnatural stimulation that do not reflect the heel-to-toe motion during gait.

3.6.5 Limitations

Currently, recordings from eight individual afferents has been presented. While this is only a small number of afferents, the lengths of the recordings for each afferent were often over five minutes, with a range of stimulation implemented, including ramps with different rates of loading, different force peaks and overloading procedures. This has provided a great depth of stimulation and response relationships to be observed across a diverse set of pressure and derivative combinations. While these recordings are long, and the afferents cover numerous regions of the foot, the inclusion of additional afferents, across all classes, would aid in further deciphering the role of tactile feedback during natural behaviours. Increasing the pool of afferents would also aid the model fitting process. Currently, this study has successfully replicated the response patterns, covering the range of pressure-response relationships seen within the experimental data presented. However, the range of responses across individuals, and afferents located in different regions of the foot, may be greater than what has been identified in the present study.

This study aimed to provide stimulation orthogonal to the skin surface, with target values considering force in this direction only. However, the handheld stimulation used to apply stimulation with high rates change, similar to those experienced during everyday behaviour, is susceptible to leading to forces also being applied tangentially, which was not considered in the present study. Future research should implement high resolution force recordings in both normal and tangential directions, to further disentangle the contributions of pressure and shear forces to cutaneous responses.

3.7 Code availability statement

All code used in this study can be found at DOI: *10.17605/OSF.IO/AHGZE*.

3.8 Author contributions

L.D.C., L.R.B., and H.P.S. conceived and designed research; E.E.H, , N.D.J.S. and L.R.B. performed experiments; L.D.C., E.E.H, A.V.V., N.D.J.S. processed data; L.D.C. analyzed data; L.D.C. and H.P.S. interpreted results of experiments; L.D.C., prepared figures; L.D.C., A.V.V. and H.P.S. drafted manuscript; L.D.C. and H.P.S. edited and revised manuscript.

3.9 Supplementary material

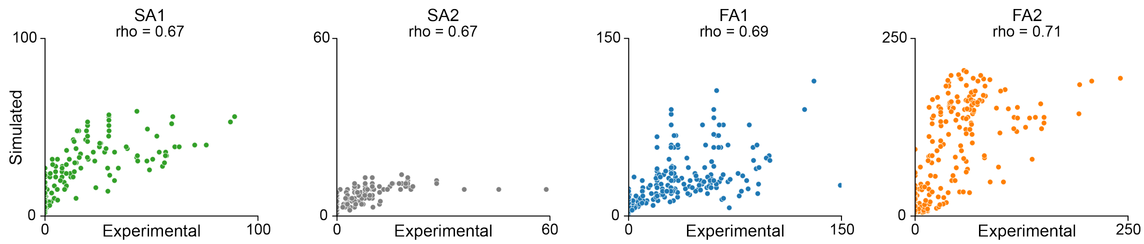

Figure S3.1: **Model performance in response to vibrations.** Correlations between experimental and simulated firing rates for SA1 (far left), SA2, FA1, and FA2 (far right) afferents.

Chapter 4

Texture perception at the foot sole: Comparison between walking, sitting, and to the hand

Chapter 2 investigated the input to the tactile system during natural behaviour, and Chapter 3 simulated the population responses to such stimuli. Both chapters have raised important considerations for the tactile system: Chapter 2 showed that the spatial signal experienced by foot sole on rough differences is very different to those experienced on flat surfaces. Chapter 3 showed that cutaneous afferents are responsive to dynamic stimulation when the magnitude of the pressure experienced by the foot is much higher than that experienced by the hand.

However, how rough surfaces, which increase spatial complexity, are perceived by the foot sole was unknown. In addition, how such high pressures, which still lead to strong mechanoreceptor responses, impact on the high resolution of tactile perception at the hands, was also unknown. These two factors, which are often faced in combination when walking on a variety of surfaces during everyday life, are received simultaneously by the tactile system, and are used to ensure that balance is maintained. This reuses a number of important questions: How do these factors impact perception? Can the foot perceive textures that are similar in properties? Do the high pressures experienced by the foot impact on perception?

This chapter, published in the Journal of Neurophysiology, addresses tthese gaps by investigating how different surfaces that are encountered during daily life are perceived along three textural dimensions: roughness, hardness and stickiness. Through comparisons to the hand, it is possible to understand how well the tactile system maintains perception across body regions and during natural interactions, which include under high forces with the feet. Understanding textural perception carries great importance due to the increasing number of interventions involving textured insoles. For textured insoles to be effective, a robust relationship between perception of the texture, and perceptions of balance, must be present.

Cleland, L. D., Rupani, M., Blaise, C. R., Ellmers, T. J., & Saal, H. P. (2024). Texture perception at the foot sole: Comparison between walking, sitting, and to the hand. Journal of Neurophysiology.

4.1 Author affiliations and contributions

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When thinking about how humans use our feet, I considered the many textures that are encountered. This served as my inspiration for conceptualising the project presented in this chapter, which I pitched to Dr. Hannes Saal as my supervisor. I purchased numerous textures that are experienced during everyday behaviour, and led the design of the protocol. Specific wording of the questions presented to participants was guided by Dr. Hannes Saal, and I approached Dr. Toby Ellmers for his expertise relating to balance and perceptions of stability.

I generated the protocol design, with the layout of textures, and participant instructions, and data input sheets in a way that ensured a repeatable and reliable approach to data collection given the high numbers of individual texture presentations. I was assisted by Mia Rupani and Celia Blaise, an undergraduate and postgraduate research assistant within the Active Touch Laboratory, during data collection, who guided participants through the stepping protocol and helped ensure reliable recordings of participant's perceptual ratings.

I performed all data processing, management, analysis and visualisation, generating simple but effective visualisations to portray the story of the paper. During this, I received supervisory feedback from Dr. Hannes Saal. I led the writing of the manuscript, alongside Dr. Hannes Saal and Dr. Toby Ellmers. Dr. Hannes Saal and I worked on revisions following reviewer comments.

The resulting paper also became the subject of an editorial review (Ackerley, 2024).

4.2 Abstract

We frequently interact with textured surfaces with both our feet and hands. Like texture's importance for grasping, texture perception via the foot sole might provide important signals about the stability of a surface, aiding in maintaining balance. However, how textures are perceived by the foot, and especially under the high forces experienced during walking, is unknown. The current study builds on extensive research investigating texture perception at the hand by presenting everyday textures to the foot while stepping onto them, exploring them with the foot while sitting, and exploring them with the hand. Participants rated each texture along three perceptual dimensions: roughness, hardness, and stickiness. Participants also rated how stable their posture felt when standing upon each texture. Results show that perceptual ratings of each textural dimension were highly correlated across conditions. Hardness exhibited the greatest consistency and stickiness the weakest. Moreover, correlations between stepping and exploration with the foot were lower than those between exploration with the foot and exploration with the hand, suggesting that mode of interaction (high vs. low force) impacts perception more than body region used (foot vs. hand). On an individual level, correlations between conditions were higher than those between participants, suggesting that differences are greater between individuals than between mode of interaction or body region. When investigating the relationship to perceived stability, only hardness contributed significantly, with harder surfaces rated as more stable. Overall, tactile perception appears consistent across body regions and interaction modes, although differences in perception are greater during walking.

4.3 New & Noteworthy

We frequently interact with textured surfaces using our feet, but little is known about how textures on the foot sole are perceived as compared with the hand. Here, we show that roughness, hardness, and stickiness ratings are broadly consistent when stepping on textures, exploring them with the foot sole, or with the hand. Hardness also contributes to perceived stability.

4.4 Introduction

Imagine waking up in the middle of the night and needing to use the bathroom. Navigating through the darkness and relying on our sense of touch, our feet effectively detect subtle differences in texture, allowing us to differentiate between the rough fabric of the bedroom carpet, the hardwood floor in the hallway, and the smooth surface of the bathroom tile. Are such judgments made through our feet comparable with texture percepts arising from our hands? The feet differ from the hands in their tactile innervation, their mechanical behavior, and in how they typically interact with surfaces, but how perceptually relevant these factors are is hard to answer. The vast majority of research on texture perception has focused on the hands and comparatively little is known about whether and how texture perception differs across body parts, though some differences between hairless and hairy skin have been established (Ackerley et al., 2014).

Both the palmar hand surface and the foot sole are hairless skin and therefore show similar innervation characteristics. Notably, though, the foot sole contains only a quarter of the number of tactile afferents compared with the hand (Corniani and Saal, 2020), yielding markedly lower spatial acuity (Mancini et al., 2014). This might affect the perception of roughness, which relies on a spatial code for coarser textures (Weber et al., 2013). Indeed, the perception of roughness has been found to differ across hand regions (Gescheider and Wright, 2021), suggesting afferent density contributes to differences in texture perception.

There are also differences in the mechanics of the skin between the hand and the foot. Specifically, skin on the foot sole is thicker (Chao et al., 2011), harder, and more variable, than palmar skin (Falanga and Bucalo, 1993; Strzalkowski et al., 2015b). It has been shown that skin stiffness directly affects discrimination accuracy for the softness of different materials (Li and Gerling, 2023), with greater stiffness leading to poorer compliance discrimination. This suggests that perception at the foot may be poorer compared with the hand due to differences in skin mechanics.

Finally, one of the largest differences between natural interactions with the external world

Figure 4.1: **Overview of the textures and presentation conditions. a)** A section (roughly 10x10cm) of each of the 16 everyday textures used, in the experimental grid layout. **b)** Illustration of the three presentation conditions, stepping with the foot (top), exploration with the foot (middle) and exploration with the hand (bottom).

involving our hands and feet is the mode of interaction. Texture exploration using the hands involves relatively low forces (Smith et al., 2002b) and typically includes lateral movement between the skin and the surface (Callier et al., 2015; Lederman and Klatzky, 1987), whereas the most common mode of interaction with the foot is arguably during walking, which involves much higher forces and less lateral movement. The force applied to a surface is especially important when judging roughness (Hollins and Risner, 2000; Lederman and Taylor, 1972), with higher forces leading to greater roughness ratings (Lederman and Taylor, 1972; Smith et al., 2002a). As the foot regularly experiences forces exceeding three times body mass (Cleland et al., 2023; McKay et al., 2017), materials may be perceived as much rougher at the foot sole than at the hand.

Investigating texture perception on the foot sole is important, because textures might provide important clues about the stability of a given surface. For example, in the hand, textures have direct functional consequences for the effective interactions with objects, enabling us to hold objects without them slipping by applying the appropriate force to ensure optimal friction between our fingers and the object (Johansson and Flanagan, 2009; Westling and Johansson, 1984). The ability to distinguish between surfaces is equally important at our feet, to be able to inform us of the surface we are standing or walking on. Decoding such information allows humans to walk on stable surfaces and adjust gait to prevent falls, for example if the ground is soft or slippery (Schepers et al., 2017). Research has also suggested that increased tactile feedback from the foot sole aids balance: for example, standing on surfaces that contain small textured elements reduces participants' natural sway (Hatton et al., 2011; Qiu et al., 2012; Wheat et al., 2014), even though these surfaces are not inherently more stable. This effect is exploited by textured insoles that aim to improve balance (Aruin and Kanekar, 2013; Hatton et al., 2022). It has been suggested that presenting textures to the foot sole will increase tactile feedback, resulting in greater information relating to shifts in pressure (Fabre et al., 2021). In turn, these cues will improve balance and reduce the risk of falling (Kenny et al., 2019a). However, which textures might be especially suited for such purpose is not entirely clear. In the hand, surface roughness is highly correlated with neural activity (Lieber et al., 2017), suggesting that roughness might be a good proxy to identify suitable textures.

Here, we investigate how everyday textures on the foot sole are perceived compared with the hand. Participants rated textures along three perceptual dimensions: roughness, hardness, and stickiness, which are among the most prominent in texture studies focusing on the hand (Hollins et al., 2000; Okamoto et al., 2013). Our aim was to study texture perception during natural behaviors in which textures are typically encountered. Therefore, when testing the hand participants gently explored the texture with their hand while seated. In contrast, when testing the foot participants stepped onto and off each texture patch to mimic texture perception during standing and walking. To test whether any putative differences in perception were due to the body part or due to the different mode of interaction, we included a third condition where people explored the texture gently with their foot while sitting, mirroring texture exploration on the hand. Thus, if exploration with the hand and foot yield similar ratings, but differ from those when stepping onto the texture, then perceptual judgments are driven by how textures are interacted with and not the identity of the body parts. Conversely, to the extent that both conditions involving the foot yield similar ratings, but differ from the hand, then differences between those body parts (innervation,

Table 4.1: Texture properties

Texture number	Texture name	Material
1	Door mat	99.5% coir, 5% polyester
2	Rug 1	100% polyester
3	Towel	100% cotton
4	Rug 2	100% polyester
5	Cork pad	Cork, polyeurathene unbleached paper
6	Plastic place mat	Polypropylene plastic, polyethylene plastic, synthetic rubber
7	Chair pad	back: 100% polypropylene, inner: polyurethane foam 30kg/cu.m.
8	Bath mat	Natural rubber, calcium carbonate
9	Astro turf	Nylon, polypropylene or polyethylene
10	Plastic desk mat	Polyethylene plastic, EVA plastic
11	Garden deck tile	Acacia
12	Tile	Ceramic
13	Crash mat	Outer: nylon (230 gsm soft nylon polyester PU coated water resistant fabric), inner: polyurethane foam (5cm reconstituted foam + 5cm medium density foam)
14	Firm foam pad	100% foamed EVA
15	Gel pad	Polyurethane elastic fiber
16	Throw	40% lyocell, 39% acrylic, 21% polyester

skin mechanics) and not different modes of interaction are the main drivers of perception.

4.5 Materials and Methods

4.5.1 Participants

Twenty young, healthy participants (7 males, 13 females) with a mean age of 20.00 (2.66) yr with no history of sensory deficits were recruited to take part in the study. One participant did not complete the exploration condition with the hand, and therefore the within-participant comparisons between the hand and foot conditions are not analyzed for this participant. All participants provided written informed consent prior to the start of data collection. The study protocol was approved by the ethical review board of the Department of Psychology at the University of Sheffield (Protocol No. 052209).

4.5.2 Textures

Sixteen everyday textures were included in the experiment (Figure 4.1). The textures selected are commonly experienced by the foot sole and were expected to vary across perceptual dimensions. They included those experienced in the household such as rugs, those experienced outside such as artificial grass and garden decking, along with materials commonly used during insole manufacturing such as cork and gel. All texture patches were at least 25 by 22 cm in size to allow participants to step onto and stand on a given patch with both feet. The same texture samples were used across all conditions.

4.5.3 Experimental Protocol

Participants took part in three presentation conditions: "Foot-Stepping," where participants stepped onto and off of the texture, "Foot-Exploration," where participants explored the textures with the foot sole while sitting, and "Hand-Exploration," where participants explored the textures with the hand while sitting. In all conditions, participants wore a blindfold and noise-canceling headphones throughout the experimental session to remove visual and auditory influences on perception. During the stepping condition, participants were guided at all times using a guiding stick, receiving a tap on the hand to ask participants to step onto and off of each of the textures, which were laid out on the floor in a 4×4 grid. Participants were instructed to lead with their dominant foot and make a cautious step onto the texture before pausing for 2–3 s on the texture with both feet and stepping off. As soon as participants stepped off of the texture, they stated their rating of the texture along the dimension in question (see next paragraph). For the exploration conditions with the foot or hand, participants remained seated and textures were presented by the research team in front of their foot or hand. Between each presentation, participants rested their feet on a foot-rest on the chair or their hands on the edge of the table. Participants received a tap on the leg or hand to instruct them to begin, and finish, exploring the texture, stating their rating following exploration termination. As in the stepping condition, in the exploration conditions, participants were free to use both feet or hands. This protocol ensured that each texture was presented for between 2 and 3 s for all three conditions.

Participants judged each texture along one of three textural dimensions—roughness, hardness, and stickiness—in separate blocks, using free magnitude scaling, a method commonly used in previous texture research (Boundy-Singer et al., 2017; Callier et al., 2015; Gescheider, 1997; Hollins and Risner, 2000; Skedung et al., 2011). For example, for roughness they were instructed to "rate the subjective roughness using any positive number including zero, with low numbers indicating very smooth and high numbers indicating very rough surfaces." Participants were also given an example prior to the start of the first presentation: "If you rate the first surface as a three, and the second surface is twice as rough then it would be a six." The same instructions were provided for all three textural dimensions, with the wording adjusted for each dimension. For the stepping condition only, participants were asked in a separate experimental block to rate the perceived stability of each textured surface. Participants rated "how stable you feel when stepping onto, and off of, the texture. If you feel so unstable that you would fall, rate it as zero." Self-rated perceived (in)stability has been shown to correlate highly with actual postural sway values in healthy controls (Castro et al., 2019; Schieppati et al., 1999), particularly when eyes are closed (Schieppati et al., 1999), as in the present study. At the end of the block, participants were asked to rate how stable they would feel in "two-foot stance on a flat surface, feet shoulder width apart and holding onto a rail" for a comparison value against all textures. The experimenter demonstrated this stance to aid the participant in obtaining the stance.

Each experimental block contained three presentations of any given texture. A separate experimental block was run for each combination of interaction mode (3) and textural dimension (3), yielding $16 \times 3 \times 3 \times 3 = 432$ textural ratings and $16 \times 3 = 48$ stability ratings in total for each participant. To speed up the experimental protocol and to minimize potential familiarization with the textures, the three interaction modes were run in a fixed order: first stepping, which was presumed the least sensitive condition, followed by exploration with the foot and finally exploration by the hand. Textures were presented in a different pseudo-random order for each of the three textural dimension blocks, and for the stability block. The same order was kept between all blocks for a given perceptual dimension and across conditions to control for order effects and facilitate data collection via a fixed texture grid in the stepping condition. A full experiment typically took 90 min to complete.

4.5.4 Statistical Analysis

All analysis was run in Python, using Pandas (v.2.0.3), Scipy (v.1.10.1), and Statsmodels (v.0.13.5). As no strict rating scale was provided, participants were free to provide scores with no upper limit constraining perceptual ratings. Using free magnitude scaling allows participants to use a scale that feels natural for them, without being limited or biased through the use of an example of a maximum score. To ensure ratings could be interpreted across participants, each rating was normalized by dividing by the mean rating for its originating experimental block. This normalization preserves the ratio of ratings between textures, while setting the mean rating to 1 for each participant. To investigate whether participants' ratings changed between presentations in the first presentation condition (roughness while stepping) due to potential habituation or adjustment to the texture variety, repeated-measures ANOVAs were conducted for all 16 textures. There were no significant changes in rating over the course of this presentation block. Perceptual ratings were then averaged across the three repeats in each experimental block, generating a "mean ratio" for each texture-condition-dimension-participant combination, with this value used for all further analyses. Textures were then ranked based on this rating. This study aimed to identify differences between texture ranks, and therefore implemented nonparametric analyses to investigate such differences.

For the group-level analysis, normalized perceptual ratings were averaged across all participants and Spearman's Rho correlations were then calculated between conditions.

For the participant-level analysis, within-participant Spearman's Rho correlations were calculated for each participant. Repeated-measures *t* tests were conducted on these correlations to identify whether perceptual ratings were more similar across some conditions than others.

To investigate how similar perceptual ratings were across participants, Spearman's Rho correlations were calculated between every pair of participants (190) for each condition and textural dimension (6). To investigate whether there were significant differences between correlations coefficients between-condition and between-participants, each *r* value was transformed using Fisher's z-transformation before being compared using two-sample *t* tests.

Repeated measures, nonparametric Friedman's tests were run to identify whether there were significant differences in texture ranks on a given perceptual dimension between conditions. A significant Friedman's test was followed up by nonparametric post hoc Wilcoxon tests, with a Bonferroni correction applied to account for multiple comparisons, yielding a corrected *P* value of 0.016.

To test whether the fact that some textures showed differences in their perceptual ratings across multiple textural dimensions could be explained by chance, we ran a Monte Carlo simulation over 100,000 trials: we randomly sampled textures from three sets independently and calculated how often these textures cooccurred at the same or a greater rate than found experimentally to generate a *P* value for the null hypothesis assuming independence.

To investigate the relationship between the perception of textural properties and participants' perception of stability, a linear regression was run to investigate the contribution of the three textural properties (roughness, hardness, and stickiness) in explaining perception of stability ratings during stepping onto and off of each texture.

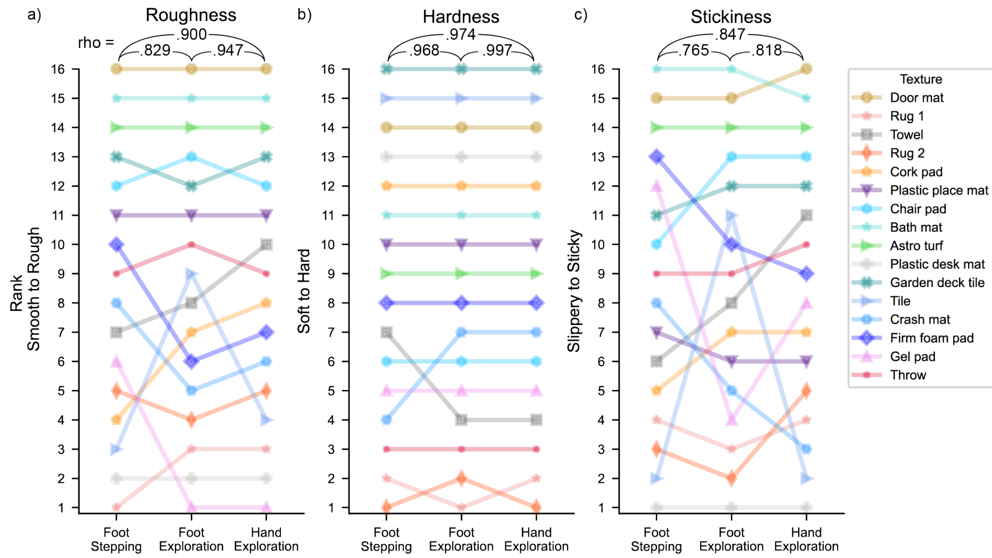

Figure 4.2: **Group-level perceptual ratings across different interaction conditions.** Slope charts showing texture ranks calculated from normalized perceptual ratings averaged across participants for roughness, **b)** hardness, and **c)** stickiness. Spearman's Rho correlations between conditions displayed at the top of each plot. All correlations are significant with $P < 0.001$.

4.6 Results

We presented 16 textures to 20 participants across three different conditions: "Foot-Stepping," where participants stepped onto and off a texture with bare feet; "Foot-Exploration," where participants explored the textures with their feet while sitting; and finally "Hand-Exploration," where participants explored the textures with their hands (see Section 4.5 for details). In each condition, participants judged the roughness, hardness, or stickiness of the textures in separate experimental blocks using free magnitude scaling.

4.6.1 Group-Level Results

As the different interaction conditions were run in separate blocks, most of the subsequent analysis will consider each texture's rank for the textural dimension in question to allow meaningful comparisons across conditions. In a first analysis, we averaged textural ratings after normalizing them across all participants and then compared their ranks across interaction conditions.

We found that perceptual ratings for each textural dimension were highly correlated across conditions (Figure 4.2). Hardness was the most highly correlated dimension (all $r>.96$), with texture rankings nearly identical whether participants stepped onto them, or explored them with their feet or hands (Figure 4.2b). For roughness, perception of very rough materials was consistent across conditions, although there was greater disagreement for smoother textures. Correlations were lower between the two foot conditions compared with the exploration conditions, though overall agreement was still high (all $r>.82$). Stickiness ratings were the least consistent across conditions (all $r>.76$), with one texture (tile) moving by nine ranks when explored with the foot.

Overall, although textures were generally ranked similarly, independent of body region or mode of contact, the correlation between the two foot conditions was sometimes lower than the correlation between the foot and hand exploration conditions, suggesting a stronger impact of mode of interaction on perception than body region.

4.6.2 Consistency within and across Participants

Next, we investigated whether and how the responses of individual participants were correlated between conditions and with those of other participants.

The participant-level results mirrored the group-level ones in that perceptual ratings were generally highly correlated across different conditions (Figure 4.3a). Again, the correlation between the hand and foot exploration was in some cases higher than the correlations involving the stepping condition (foot/hand exploration vs. stepping/hand exploration for hardness: $t=3.69$, $p=.002$; foot/hand exploration vs stepping/foot exploration for stickiness: $t=2.30$, $p=.034$; see Figure 4.3a). This suggests a stronger impact of mode of interaction on perception than body region, when there were differences between these conditions.

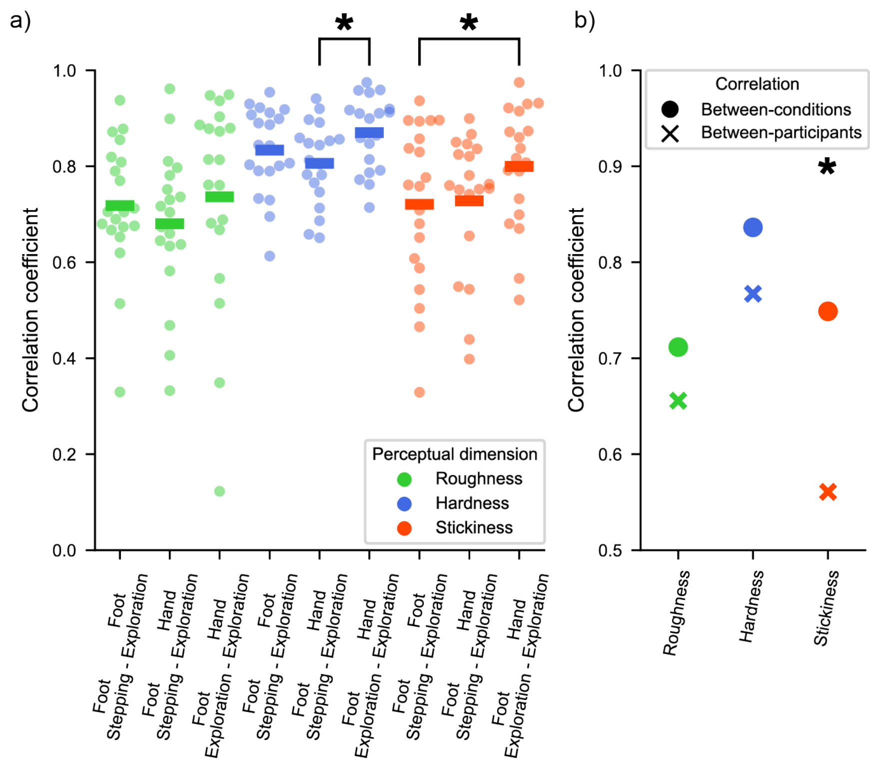

Figure 4.3: **Between-participant and between-condition correlations. a)** Between-condition correlations for each participant. Each point represents the correlation in perceptual ratings between two conditions for a given participant. The horizontal line represents the mean correlation across all participants. *Significant repeated-measures *t*-test (P<0.050), indicating a difference in the between-condition correlation coefficients. **b)** Comparison of average between-participant (crosses) and between-condition (circles) correlations for each perceptual dimension. *Significant difference.

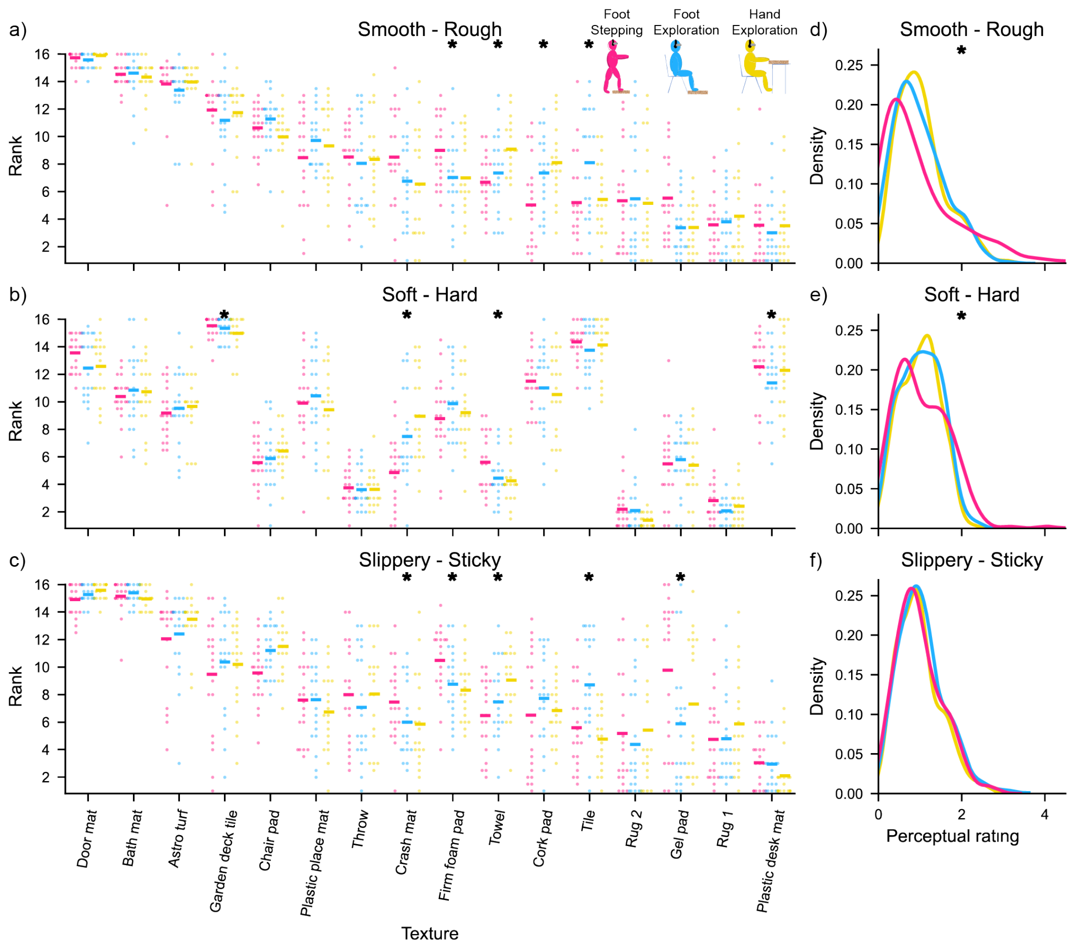

Figure 4.4: **Differences in perception between conditions.** *Left:* Participant rankings for each texture for **a)** roughness, **b)** hardness and **c)** stickiness, sorted by mean roughness rating. Mean ranks are indicated by horizontal lines. Individual points denote ranks for single participants. *Significant Friedman's tests showing a difference in ranks between conditions. *Right* Kernel density plots showing the distribution of responses for **d)** roughness, **e)** hardness and **f)** stickiness. *significant Levene's tests for equal variance.

Notably, average participant-level correlations between conditions were greater than those between participants (Figure 4.3b). Comparing the correlation coefficients across participants with those obtained within participants (see Section 4.5), stickiness ratings were significantly less consistent between participants than between interaction conditions within the same participants (t=2.39, p=.017). Although the same pattern exists for roughness (t=0.74, p=.462) and hardness (t=1.38, p=.169), the differences between were not statistically significant. Thus, texture perception is at least as consistent between body regions and modes of contact within a given participant, than it is between participants in the same condition.

Table 4.2: Post hoc Wilcoxon tests run on textures with significant Friedman's test. Statistic show W value. *P<0.050; **significant following Bonferroni correction for multiple comparisons, P<0.016. All significant values (marked as * or **) are rendered in bold.

Dimension	Texture	W-S	W-H	S-H
Roughness	Firm foam pad	**33.5****	**31.5***	85.5
	Towel	63.5	**24.5****	49.5
	Cork pad	**36.5***	**23.5****	69.0
	Tile	**18.0****	66.0	**32.5****
Hardness	Garden deck tile	34.5	23.0	44.0
	Crash mat	**3.0****	**1.0****	**34.5***
	Towel	**23.0***	**32.0***	48.0
	Plastic desk mat	46.0	48.0	47.0
Stickiness	Crash mat	**34.0***	47.0	59.0
	Firm foam pad	**38.0***	**22.0****	77.5
	Towel	32.5	**21.0****	**35.0***
	Tile	**22.0****	73.0	**21.0****
	Gel pad	**13.0****	37.0	**28.0***

4.6.3 Differences between Interaction Conditions

Next, we further investigated differences between interaction conditions, by testing whether texture ranks differed significantly between conditions. For roughness, Friedman's tests revealed significant differences for four textures in the middle of the smoothness-roughness spectrum (Figure 4.4a). Post hoc tests revealed that almost all differences occurred between the stepping condition and either the foot or hand exploration conditions. Only one significant difference, for the tile, occurred between the foot and hand exploration conditions (see Table 4.2 for details). For hardness, Friedman's tests revealed significant differences in rank for four textures (Figure 4.4b), though post hoc tests were only significant for two textures. Again, most of the differences involved the stepping condition. Finally, for stickiness perception, significant differences were found for five textures (Figure 4.4c), with these spread relatively equally across conditions. Overall, as differences more often involved the stepping condition, this might suggest that they were driven more by the mode of interaction (low vs. high force) rather than the fact that a different body region was involved (hand vs. foot), in agreement with our earlier observations.

Notably, when a texture was judged differently across conditions, this often occurred along multiple textural dimensions: the towel yielded significant differences across all three textural dimensions, and the tile, firm foam pad, and crash mat differed across two dimensions each. Indeed, Monte Carlo simulations confirmed that these cooccurrences were unlikely to arise when assuming independence across textural dimensions $P = 0.006$, see Section 4.5 for details), suggesting that a texture yielding a perceptual difference across one textural dimension was likely to do so across another.

So far, our analysis has focused on texture ranks, rather than their ratings directly. Since ratings were collected in different blocks for different interaction conditions, they might not be directly comparable. However, we can instead investigate whether the spread of responses, e.g., how much rougher the roughest texture feels compared with the smoothest one, differs across conditions. We found that the spread of perceptual scores differed between presentation conditions for roughness and hardness (Levene's tests of equality of variance; $F = 17.63$, $P<.001$ and $F = 15.36$, $P<.001$, respectively, Figures 4.4d, e). Specifically, perceptual roughness ratings during stepping were spread further (Figure 4.4d) compared with foot and hand exploration. On average, the roughest texture was rated as just over 10 times rougher than the smoothest texture during stepping. In contrast, during foot and hand exploration, the roughest texture rated at just over, and just under, five times as rough as the smoothest texture, respectively. This suggests that roughness levels were magnified when walking, making textures seem rougher than when perceiving them with the hand or under low forces during exploration with the foot. The same pattern was evident for hardness perception, with increased spread of the responses during stepping. In contrast, the distribution of responses for stickiness perception was equal across all conditions ($F = 0.37$, $P=.692$, Figure 4.4f).

4.6.4 Textural Dimensions and Stability Ratings

To investigate whether and how any of the textural dimensions are related to perception of stability, we regressed average perceptual ratings for the different textural dimensions onto the

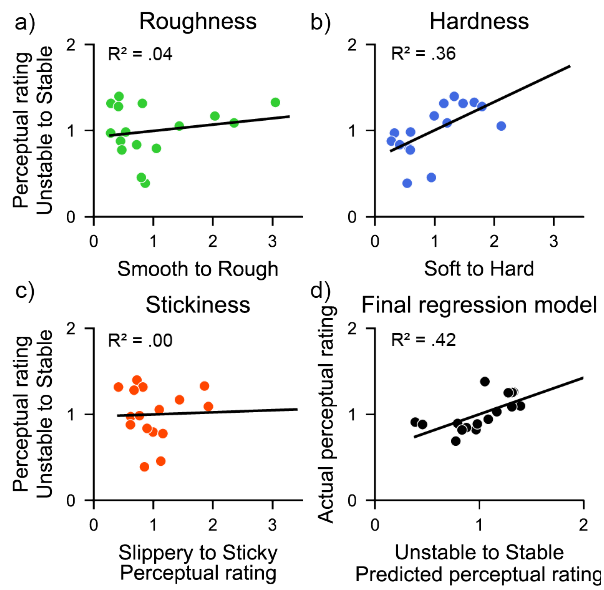

Figure 4.5: **Relationship between textural dimensions and perceived stability. a)** The relationship between perceived roughness and stability. **b)** The relationship between perceived hardness and stability. **c)** The relationship between perceived stickiness and stability. **d)** Predicted stability ratings from the multiple linear regression model compared to recorded ratings of stability. Each point reflects a single texture, showing average scores across all participants. Lines denote lines of best fit.

stability ratings for each texture, both independently and jointly. For roughness, stability ratings quickly plateaued with increasing roughness (Figure 4.5a), leading to low explanatory power ($R^2 = 4\%$). The relationship between hardness and stability appeared linear (Figure 4.5b), with perceived stability growing with increasing hardness, explaining 36% of the variance in stability ratings. There was no evident relationship between stickiness and perceived stability (Figure 4.5c; $R^2 = 0\%$). Finally, running a multiple linear regression, using roughness, hardness, and stickiness as input variables and stability as the output variable explained 42% of the variance in stability ratings. However, only hardness contributed significantly ($P = 0.05$).

4.7 Discussion

The current study investigated texture perception at the foot sole, investigating three textural dimensions—under different contact conditions (stepping vs. gentle exploration with the foot sole) and body region (foot vs. hand). On both the group and individual level, perception was highly correlated across all conditions and textural dimensions. In fact, correlations between conditions were stronger than correlations between participants, indicating more consistent ratings within a given participant across interaction mode and body region than between different individuals for the same condition. Nevertheless, a subset of individual textures showed systematic differences across conditions, with the biggest shifts induced by the stepping condition. Texture ratings were also spread more widely in this condition, suggesting that most of the differences in texture perception observed on the foot is likely due to the difference in contact mode rather than an inherent property of this skin site. The results also suggested that hardness is the only perceptual dimension that contributes to participants' perception of stability, with neither roughness nor stickiness ratings yielding significant correlations.

4.7.1 Body Region

We found that texture perception was broadly consistent between the hand and the foot, with high correlations between all tested conditions for all three textural dimensions. Indeed, when there were differences, these were rarely grouped by body region, but instead appeared to depend on specific modes of interaction (such as stepping, see further discussion in Section 4.7.2). In agreement with these findings, correlations between conditions within the same participants were generally higher than those between participants. At the same time, the between-participant correlations in the present study were comparable to those established previously. For example, Richardson et al. (2022) used a comparable set of everyday textures, which they asked participants to explore actively with their hands. The authors found a correlation of $r = 0.70$ in similarity ratings between participants, which the results of the present study are in line with. The observed consistency between body regions is surprising, given the differences in innervation density and skin mechanics between both regions, and might suggest a central mechanism to maintain perceptual constancy across the hairless skin on the body. Future research should further investigate the extent of perceptual constancy across more body regions, extending to hairy skin sites (see Ackerley et al., 2014).

4.7.2 Mode of Interaction

We found that changing the mode of interaction, from gentle exploration with the foot sole to stepping onto and off the texture, led to greater changes in texture perception than using a different body region, that is switching from the hand to the foot. This difference was manifested in lower correlations of perceptual ratings in the stepping condition with the other two conditions, but also an expansion in the range of responses for roughness and hardness.

One major difference in the stepping condition was arguably the much higher forces acting on the foot during stepping compared with seated exploration, which might explain some of these differences. Indeed, texture perception on the hand is known to depend on the force applied, with higher forces increasing the perception of roughness (Lederman and Taylor, 1972; Smith et al., 2002a). However, forces investigated in previous research on the hand are minute compared with those experienced by the foot during everyday behavior, which regularly exceed body mass more than threefold (Cleland et al., 2023). Another difference was that participants were able to use exploratory stroking movements when touching the texture with their hand or the foot when seated. Such active exploration has been shown to influence texture perception on the hand when compared with static presentation, for example for stickiness (Grierson and Carnahan, 2006) and roughness (Hollins and Risner, 2000). Moreover, different types of active exploration, such as stroking or pushing have also been shown to alter perception (Yokosaka et al., 2020). When walking, deliberate low-force exploratory movements are not possible. However, walking might also not resemble static presentation conditions, because the foot does not touch the ground uniformly and at the same time. Instead, the rolling motion during foot placement (where the heel strikes the ground before the mid-foot) and push off (where the mid-foot leaves the floor before the toes) causes significant shear forces (Crossland et al., 2022; Tappin and Robertson, 1991), which might provide rich temporal information. Nevertheless, despite the differences seen in the stepping condition, these were relatively small, suggesting that texture perception is broadly similar across all interaction conditions.

4.7.3 Relating Textural Dimensions to Stability

Humans must be able to maintain balance when walking or standing on range of surfaces to prevent falls and subsequent injury. Textural cues might provide relevant, rapid hints regarding the current surface, and therefore contribute to perceived stability. For example, slippery or very soft surfaces might be perceived as less stable. However, out of the three textural dimensions investigated in the current study, only hardness contributed significantly to perceived stability, explaining 40% of total variance in stability ratings, with harder surfaces rated as more stable. Previous research has reported similar decreases in perceived stability in older adults when standing on soft (e.g., foam) rather than hard surfaces (Anson et al., 2019). Interestingly, when controlling for actual changes in postural sway, older adults who had previously fallen experienced the greatest decreases in perceived stability from hard-to-soft surfaces. The authors suggested that this may have been driven by increased fear of falling experienced by those who had previously fallen, given that experimentally induced fear of falling is known to make people feel less stable (Cleworth and Carpenter, 2016; Ellmers et al., 2022). Future work should look to explore if these relationships are driven by changes in hardness perception. For instance, do older adults who have fallen rate "hard" textures as softer, and does this underpin the more pronounced changes in perceived stability when standing on soft surfaces? Does fear of falling alter our perception of texture hardness, leading to textures previously perceived as hard to now be experienced as softer? Recently developed virtual reality paradigms (Cleworth et al., 2016; Ellmers et al., 2024; Raffegeau et al., 2020) could help answer these questions.

Neither roughness nor stickiness showed any relationship with perceived stability in the present work. This might suggest that texture only plays a limited part in perceived stability or that these cues are processed in a more complex, perhaps nonlinear way. However, it should be noted that the textures used in the current study did not pose any serious threat to participants' stability. For example, no extremely rough, unstable (e.g., gravel) or extremely slippery surface (soapy, wet tile) was included in the study. It is therefore possible that texture at the extreme ends of the spectrum does play a greater part in the perceived stability. Nevertheless, even the textures used in the current study yielded a wide range of stability ratings, which could not be fully explained by textural ratings alone. It should be noted that the three dimensions tested here do not fully cover the perceptual texture space and other textural aspects might still contribute to stability.

Recent research has begun to explore the use of textured insoles to improve balance (e.g. Aruin and Kanekar, 2013; Hatton et al., 2022; Robb and Perry, 2022), following the hypothesis that increased tactile feedback aids balance. Such textured insoles have been shown to reduce postural sway (Kenny et al., 2019b), especially when standing on an unstable surface such as foam (Qiu et al., 2012). The majority of these interventions currently focus on using rough textures; as we did not find any relationship between roughness and perceived stability per se, it is likely that these insoles act via a more indirect mechanism, such as generally elevating the level of tactile feedback and subsequent muscle activity (Robb et al., 2021; Robb and Perry, 2022). Indeed, roughness is highly correlated with neural activity in the hand (Lieber et al., 2017), suggesting that textures perceived as very rough might make good candidates for insoles, taking into account the fact that they will feel even rougher during walking, as shown in this study.

4.7.4 Limitations

The current study aimed to strike a balance between presenting a diverse set of textures, assessing texture perception along multiple textural dimensions, and allowing for broad comparisons between the foot and the hand, but also different modes of texture interaction of the foot itself. As such, the texture set was necessarily limited. For example, we only used textures that did not pose any serious threat to participants' stability to ensure the safety of participants and maintain a focus on texture perception. As a consequence, the relationship between texture and stability needs to be interpreted with this limitation in mind and it is possible that more challenging or balance-threatening textures might contribute differently to stability (see discussion aforementioned). The textures were selected as they are commonly encountered in everyday life. However, as a consequence, their properties were not carefully controlled, as is possible with artificial texture sets, and their overall diversity precludes testing the perception of subtly different textures. Although one prior study has investigated the ability to discriminate between similar textures (Ofek et al., 2018), further research is required to get a complete picture regarding the capability of the tactile system on the foot sole. Such future research might also directly compare texture perception on different body parts or via different interactions by presenting participants with pairs of textures during a single trial. However, such experiments are data-intensive; in the present study, our focus was on investigating texture perception on the foot sole as broadly as possible. Our aim was to focus on conditions that mimic natural interactions with textures as closely as possible (e.g., walking). Although this strategy ensured behavioral relevance, comparisons across conditions need to be interpreted with care. For example, although contact force was a major difference between the stepping and exploration conditions, these also differed in other, potentially relevant, aspects, such as the presence of dynamic motion between the texture and the skin. Future studies might include passive stimulation or better controlled active conditions (such as purely static presentation of the textures or including a high-force condition on the hand) to isolate the contributions of these different effects. A final limitation relates to the lack of objective postural stability measure (e.g., trunk instability when stepping onto or off the textured surfaces). However, as we were interested in how different textures affected perceptual outcomes (rather than posture itself), we do not deem this a major limitation. Furthermore, previous work has shown strong correlations between perceived and objective postural (in)stability outcomes (Castro et al., 2019; Schieppati et al., 1999)—particularly when eyes are closed (Schieppati et al., 1999), as in the present study. Nonetheless, future work should look to explore how texture perceptions interact with objective postural control outcomes..

4.8 Data Availability

All raw data and code used to analyze the data can be found at: https://doi.org/10.17605/OSF.IO/SP8K2.

4.9 Grants

L.D.C. was supported by a studentship from the MRC Discovery Medicine North (DiMeN) Doctoral Training Partnership MR/ N013840/1. T.J.E. was supported by a Wellcome Trust Sir Henry Wellcome Fellowship 222747/Z/21/Z. H.P.S. was supported by Leverhulme Trust Research Project Grant RPG-2022-031.

4.10 Disclosures

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

4.11 Author contributions

L.D.C., T.J.E., and H.P.S. conceived and designed research; L.D.C., M.R., and C.R.B. performed experiments; L.D.C. analyzed data; L.D.C. and H.P.S. interpreted results of experiments; L.D.C. prepared figures; L.D.C., T.J.E., and H.P.S. drafted manuscript; L.D.C., T.J.E., and H.P.S. edited and revised manuscript.

Chapter 5

General discussion

5.1 Introduction

Combining computational and experimental techniques from psychology, neuroscience and biomechanics, this thesis has investigated the role of tactile feedback from the foot during natural behaviour and the resulting contributions to balance maintenance, looking at three stages of the processing timeline. Firstly, Chapter 2 characterised the input to the tactile system during everyday behaviours through the use of pressure sensitive insoles. Due to the high resolution insoles, the spatial complexity of the signals was analysed during a wider range of behavioural activities than has been investigated before. Secondly, by combining experimental and computational techniques, Chapter 3 investigated cutaneous afferent responses to high-pressure stimuli that are reflective of those experienced during gait. Finally, perception of textures experienced during everyday life was explored under different loads and body regions in Chapter 4. Taken together, this thesis demonstrates the ability of the tactile system to encode complex inputs encountered when walking on rough, soft and slippery surfaces, regardless of the forces applied during the interaction. Cutaneous receptors are shown to be able to encode responses to high force stimulation, combining this with spatial information from the surfaces we stand or walk upon, to provide us with important information not relayed by other senses that can be used to maintain balance.

Throughout this thesis, the results from each study have been discussed within each chapter. This final chapter is a more general discussion, reviewing the findings from the thesis in a wider context, considering four main areas: shear forces, the interplay between sensory systems, how tactile feedback changes during ageing and disease, and finally investigating how tactile feedback could be utilised to improve balance.

5.1.1 Shear forces

The foot does not receive input exclusively perpendicular to the plantar surface, but there are also an abundance of shear forces acting on the foot throughout the step cycle (Crossland et al., 2022; Jones et al., 2024; Tappin and Robertson, 1991). Shear forces activate cutaneous receptors differently depending on their class, and are the preferred stimulation type for SA2 and FA1 afferents both in the hand and at the foot sole (Johansson, 1978; Johansson and Vallbo, 1983; Knibestöl, 1973). Therefore, current research that has looked at the responses of cutaneous afferents may be under- or over-estimating the contributions of some afferent classes to balance maintenance during gait, due to the shear forces present.

5.1.1.1 Cutaneous responses to shear forces

Chapter 3 provided some insight into the responses of SA2s to high force input. With higher pressure inputs, there will be increased amounts of skin indentation, both normally and tangentially. This tangential force occurs partly due to the stretching of the skin that occurs as a result of displacements of this skin, which will be elevated due to the greater pressures being applied to the skin (Vanderhaeghe et al., 2024; Xiong et al., 2010). This, combined with the handheld stimulation used in the study may result in additional, non-normal, loading of the skin, yielding increased levels of skin stretch and shear forces. This multi-faceted stimulation was likely a contributor to a greater firing rate exhibited by SA2 afferents, in comparison to controlled low-pressure vibrations or ramp-and-hold stimuli applied perpendicular to the skin.

The greater responses identified from slowly adapting receptors were not reflected when focusing on fast adapting receptors, which also provide information regarding shear forces (Viseux, 2020). Chapter 3 demonstrated that FA1 receptors only respond up to around $5N/cm^2$, which is well below those pressures experienced during everyday life. This may be due to their location being much closer to the skin (Delhaye et al., 2018). The top layers of the skin deform quickly under lower pressures, causing corpuscle deformation, and remains lower than the deformation experienced by the deeper skin layers (Corniani et al., 2023). As a result, applying further pressure will likely not lead to additional corpuscle deformation, thus limiting the ability to respond further. It is, however, possible that due to the larger contact areas experienced during gait, up to 135cm^2 (McKay et al., 2017), result in high forces being reflected as lower pressures. Therefore, shear forces may be more evenly spread, or present on a finer scale, activating FA1s more than has been achieved experimentally so far. Additionally, as shear forces can happen at the micro-scale and are detectable during movement (Crossland et al., 2022; Ito et al., 2017; Jones et al., 2024), it is highly likely that FA1 afferents will sense these and provide input to the feedback loop to prevent a loss of balance.

5.1.1.2 Contributions of shear to perception

Being able to detect surfaces is essential due to the effects this can have on walking strategies, which are more cautious when faced with uneven, unstable, or slippery surfaces (Cleland et al., 2023; Kent et al., 2019; Menant et al., 2009; Whitmore et al., 2016). While a plan can be made regarding strategies, these more cautious strategies will only be confirmed once the environment has been identified, and while visual input will provide individuals with an indication of the surface they are walking on, haptic input increases the accuracy of perception (Heller, 1982).

Shear forces contribute to the ability to detect and decode the surfaces upon which we stand and walk on. In the hand, when interacting with surfaces, humans opt to explore textures by sliding their fingers across the surface (Callier et al., 2015), with this sliding motion leading to better discrimination of rough surfaces (Roberts et al., 2020). Sliding your finger across a surface while applying force to the surface leads to slip and shear, as well as resulting in vibrations that ripple across the skin further away from the contact point, including down the forearm (Tummala et al., 2023). Smaller movements that occur during object grasping that elicit a degree of shear have also been shown to increase perceptual discrimination of surface friction (Afzal et al., 2023). As shear forces are prevalent, despite no active exploratory moments, skin stretch will occur throughout the gait cycle. Therefore, generalising these findings from the hand to the foot, shear forces are beneficial to perception and can explain the high correlation in perception between the foot and hand observed in Chapter 4.

5.1.2 Sensing slips

Not only do shear forces contribute to texture perception, but shear forces, and slip, are also the first signal that will be sensed when one begins to fall. Shear forces occurs instantly and reach their maximum within 400ms of a balance perturbation (Sutter et al., 2022). The instant occurrence of shear long before it reaches its maximum is essential, as voluntary actions are not typically instigated until around 150ms after a perturbation (Latash and Singh, 2023). As the reflex responses in the lower limb occur at around 100ms after stimulation (Peters et al., 2020), this suggests that reflex responses led by tactile input allow for unconscious mechanisms to be implemented to reduce the chances of falls. Therefore, tactile sensitivity to shear is an important component of perception and encoding at the foot sole.

The direction of the slip is also important, as this contains information that can be used to guide the appropriate adjustments of pressure: if the slip occurs where one's foot slides forwards away from the body during heel strike, the slip leads to forces moving and the skin slipping towards the body. Here, centre of mass should be moved forwards to prevent one from falling backwards. In the hand, direction preference has been observed, with tactile mechanoreceptors responding more strongly to forces applied in given directions (Birznieks et al., 2001). Specifically, SA2 and FA1 afferents were found to be tuned to forces in the proximal direction. This directional sensitivity has also been demonstrated in SA2 afferents in the foot sole, with the directional preference varying for afferents across the foot (Kennedy and Inglis, 2002). As a result, SA2 and FA1 afferents will provide an important contribution to balance control, should a slip occur, due to their preference for shear stimulation and directional tuning.

While the role of shear can only be speculated about based on the findings from the results presented within this thesis, future research should systematically investigate how shear, to different degrees, activates tactile mechanoreceptors. Identifying the strength of reflex responses in lower limb muscles would also help to disentangle the role of tactile feedback in the balance control pathway.

5.2 Interplay between sensory systems

Multiple sensory systems are involved in balance control, each of which communicates with the others in order to implement the appropriate strategy to remain upright and prevent falls . An example of this occurs following a slip when stepping onto ice: first, the tactile system must sense slip in the form of skin shear and stretch, and rapid pressure changes, before the proprioceptive system simultaneously senses unexpected joint angles and lengthening of the lower limb muscles. While this happens, the head moves backwards, triggering vestibular responses originating from the inner ear. Visual signals will also provide information regarding the degree of slip. Taken together, information from each of the four sensory systems allows for the appropriate balance control mechanisms to be implemented to prevent a fall from occurring.

5.2.1 Touch and Proprioception

There is a strong relationship between the tactile and proprioceptive systems, which combine to form the somatosensory system. Research has identified the presence of cutaneous reflex pathways, and it is through these pathways that textured insoles lead to alterations in muscle activity and therefore balance and gait. Here, cutaneous stimulation of the plantar sole leads to alterations of muscular responses (Aniss et al., 1992; Peters et al., 2020; Sharma et al., 2020). The specific muscles activated or suppressed by this stimulation depends on the location of the tactile stimulation on the foot sole (Nakajima et al., 2006; Robb et al., 2021; Sharma et al., 2020).

Robb et al. (2021) investigated the effect of tactile feedback during dynamic behaviour by recording muscular activity during gait termination while participants stood on a textured surface. Their findings demonstrated that the additional feedback provided by textured surfaces led to an earlier muscular response, providing evidence that tactile feedback can alter proprioceptive feedback during dynamic behaviours. Additionally, the presence of texture only at a single region of the foot is sufficient to alter proprioceptive feedback (Robb and Perry, 2022). Robb and Perry (2022) measured muscular activity in multiple lower limb muscles during locomotion, finding that not only did the location of passive stimulation applied to the foot impact activity, but these changes were also dependent on the the phase of the step cycle. For example, there was greater muscle activity during the toe-off phase of the step cycle when the texture was located at the lateral midfoot compared to no texture, suggesting that tactile feedback could be utilised to generate proprioceptive changes in specific phases of gait.

While the presence of the cutaneous reflex pathway is clear, the strength of the muscular reflex to cutaneous stimulation decreases when the foot is loaded (Nakajima et al., 2006). One reason for this may be the increased mechanoreceptor perception thresholds when standing compared to sitting (Mildren et al., 2016; Watts, 2024), which indicate higher activation thresholds. Therefore, greater stimulation would be required to activate receptors and maintain the strength of the resulting muscular responses. Due to the stronger responses to high pressure stimulation by slowly adapting receptors compared to fast adapting receptors identified in Chapter 3, it is likely that SA receptors are those that contribute most to balance control under normal conditions. However, the addition of texture may supplement the high pressures with high frequency vibrations. These vibrations are likely to activate fast adapting afferents, adding to the feedback received by lower limb muscles, and strengthening the reflex pathway.

To further overcome the high forces experienced, which may saturate FA receptors, stimulation could be applied during the swing phase of the gait cycle when the foot is not in contact with the ground. This approach has been shown to reduce sway during turning (Ravanbod et al., 2021), although significant differences were only seen in one muscle, the proneus longus. While this intervention does not lead to the supplementation of tactile information during foot placement, it demonstrates that the tactile system can be utilised in a different way that is still beneficial to balance, specifically by exploiting the relationship between the tactile and proprioceptive systems originating from fast adapting receptors responding to high frequency stimulation.

5.2.2 Input from the visual and vestibular systems

The visual and vestibular systems are also involved in balance control. The vestibular system provides information regarding head tilt, signalling acceleration, and rotation of the head (Day and Fitzpatrick, 2005); while the visual system, among other things, provides us with information relating to the environment in front of us to aid in the generation of motor patterns (Cates and Gordon, 2022). These two are interlinked during the vestibulo-ocular reflex, which aims to orient the head in such a way to maintain a steady gaze, such as during gait (Latash and Singh, 2023), which is required following a balance perturbation. However, during a controlled perturbation, Sutter et al. (2022) identified that the acceleration of the head did not reach the threshold for vestibular feedback to trigger corrective mechanisms regarding the fall, until approximately 250ms. While this is within the time during which the postural reaction occurred, this is much longer than the time taken for cutaneous reflexes to occur. Additionally, the head not moving significantly, while shear forces can be detected, means that visually guided reactions will not occur within the same timescale that cutaneous input begins. Therefore, while visual and vestibular information is important, it is preceded by tactile feedback, and cutaneous reflexes.

5.3 Effects of altered sensation with age and disease

As the first step to understanding how reductions or changes in sensation impacts behaviour, this thesis investigated tactile input, output and perception in healthy individuals. This approach provides a baseline for comparing how sensation changes following ageing or disease, and also provides metrics and components of touch that should be monitored in individuals with reduced sensation. Two common factors that lead to a decline in tactile sensation are ageing and diseases such as neuropathy, which in turn is related to changes in gait and balance.

5.3.0.1 Changes to input

As one ages, and as sensory neuropathies develop and progress, cutaneous mechanoreceptor thresholds increase (Thornbury and Mistretta, 1981), increasing the magnitude of mechanical input to the skin required to activate tactile mechanoreceptors. This is especially true in those who have recently fallen (Macgilchrist et al., 2010), indicating that the mechanical input that the receptors are receiving is not sufficient to generate adequate tactile feedback to help in preventing falls. This is likely one reason that greater pressures are implemented during gait as one gets older (Fernando et al., 2016; McKay et al., 2017; Mueller et al., 2008), employed to meet the elevated thresholds to enable sufficient tactile feedback to occur. This elevated pressure comes despite a reduction in gait speed (Wuehr et al., 2014), against the trend seen in healthy individuals. These elevated pressures and increased stance and contact times (Fernando et al., 2016), mean that the mechanoreceptors will receive a very different input compared to young, healthy populations, which in combination with the factors in Section 5.3.0.2 will alter the role of gait in balance.

5.3.0.2 Changes to output

Further changes that will also impact on balance control relate to how signals from tactile receptors are conveyed along axons of the peripheral nerves in diabetic and neuropathic populations. Due to the decrease in axon diameter (Malik et al., 2001; Yagihashi et al., 1990), and dramatic reduction in myelination (Hill and Williams, 2004; Malik et al., 2001), the time taken for cutaneous feedback to travel from the foot sole to the spinal cord is increased significantly (Deshpande et al., 2008; Di Iorio et al., 2006; Rathi et al., 2019). Additionally, some signals from cutaneous receptors may be lost before they are received by the spinal cord (Gilliatt and Willison, 1962), or even before they reach lower limb muscles as shown by a reduction in the presence of cutaneous reflexes following stimulation at the foot sole (Peters et al., 2016). Given that mechanoreceptors convey important information regarding changes in stimulation, this delay in the feedback loop may mean that falls begin before the brain, or even the spinal cord, has received information relating to the slip.

5.3.0.3 Changes to perception

In addition to the loss of reflex responses, the loss of tactile signals also impacts the ability to perceive the environments we are walking on. Despite consistent perception across the body with differing afferent densities in healthy individuals (Cleland et al., 2024; Gescheider and Wright, 2021), prior research has shown that the ability to recognise textures slows as age increases (Master et al., 2010). Additionally, perception and discrimination thresholds also increase with age (Sathian et al., 1997). This reduction in perceptual ability compounds the existing difficulties faced when walking on uneven ground, impacting on one's ability to identify the environment. If a subtle change in the environment to a less stable surface is not be detected consciously, this may result in the absence of a more cautious walking style than would otherwise be typically implemented by healthy individuals (Gates et al., 2012) to prevent them from falling.

Further impacts on perception may result from changes to the spatial complexity experienced during gait. While greater magnitudes of force are experienced by the foot sole, this does not reflect changes to the spatial complexity of pressure patterns at the foot sole, as seen in healthy individuals (Cleland et al., 2023); the changes in gait dynamics may increase the spatial complexity of signals received by the tactile system. While this may not be as problematic when walking on flat or predictable surfaces, not computing the full spatial complexity of an unstable environment may impact the time taken to instigate corrective mechanisms in the event of a loss of balance. This problem is exacerbated by a reduction in spatial acuity (Deflorio et al., 2023; Sathian et al., 1997; Stevens and Patterson, 1995) and reduced afferent density in the elderly population (Aydoğ et al., 2006; García-Piqueras et al., 2019; Kobayashi et al., 2018), and in those with reduced functioning receptors in neuropathy (García-Mesa et al., 2021; Malik et al., 2001; Sorensen et al., 2006). Given the importance of spatial components of signals in texture perception, this also indicates that basic textural recognition and perception will also be diminished; this is corroborated by prior research identifying decreased pattern recognition with increasing age (Master et al., 2010).

Another potential reason for this decrease in texture perception are alterations in skin mechanics. As one gets older, the skin gets thinner (Leveque et al., 1980; Petrofsky et al., 2008) and less elastic (Deflorio et al., 2023). The change in elasticity is especially important, given that tactile perception decreases as the skin becomes stiffer and less elastic (Abdouni et al., 2018). These changes also have a direct impact on how the mechanoreceptors are activated due to their location just below the skin surface. The resulting combinations of changes to the mechanoreceptors themselves, and the skin mechanics surrounding them, reduce the tactile system's ability to process stimuli accurately, and may lead to surfaces not being perceived correctly and thus leading to a lack of corrective mechanisms being implemented to prevent falls.

5.4 Utilising touch to improve balance

This thesis has presented an investigation of the tactile system's input, output and tactile perception during everyday behaviour, including during both simple behaviours in predictable environments and under more challenging conditions like walking on gravel. The evidence provided demonstrates that the tactile system is able to maintain its sensitivity and consider spatially complex inputs. As discussed in Section 5.3, loss of tactile sensation can have negative impacts on balance too. Here, the possibility of supplementing and restoring tactile sensation with additional feedback will be discussed.

5.4.1 Vibrotactile feedback

While the foot experiences high forces, interventions to improve balance have often used low amplitude vibrations provided to the plantar sole. The aim of providing additional feedback via vibration is to reduce tactile sensory thresholds, thus increasing sensitivity (Bagherzadeh Cham et al., 2018; Khaodhiar et al., 2003; Schlee et al., 2012; Schmidt et al., 2017; Zwaferink et al., 2020). With increased sensitivity comes increased awareness of the pressure distribution at the foot sole, and thus improved ability to sense the need to implement corrective mechanisms to maintain balance (Vuillerme et al., 2007).

Before the turn of the century, Kavounoudias et al. (1998) identified that selective spatial stimulation of the mechanoreceptors in the foot sole led to alterations in participant's centre of pressure. These alterations differed depending on the location of the foot being stimulated, but was always in the opposite direction to stimulation. For example, when the heels were stimulated, the CoP moved in the anterior direction towards the toes. This technique was one of the first to show that providing additional tactile feedback could alter balance, and therefore highlighting the importance of touch in balance maintenance. Due to the high frequency stimulation used in this study, fast adapting receptors would have been activated to a greater extent than slowly adapting mechanoreceptors. Although Chapter 3 showed that high force stimulation was not favoured by FA1 afferents, the supplementation of feedback using vibrations may activate them to a greater extent. As FA1 receptor thresholds remain stable with age (Wells et al., 2003), the use of high frequency stimulation may also be beneficial in ageing populations to compensate for reductions in sensation of other afferent classes.

Further evidence in support of supplementing baseline tactile input with additional vibrations has used vibratory insoles. In the elderly, postural sway can be reduced during standing balance when vibrations are applied (Priplata et al., 2002, 2003, 2006). Similarly, sway is also reduced in patients with neuropathy (Cham et al., 2020). As both populations possess poor tactile feedback, this additional stimulation will activate mechanoreceptors that may be otherwise silent, and enable far greater information regarding plantar pressure patterns to be received and processed.

Despite promising findings, it is important to note that the underlying mechanism behind this additional stimulation in improving balance is unknown; is it as a result of lower mechanoreceptor thresholds following stimulation or perhaps due to the resulting muscular activity resulting from cutaneous reflex loops? If stimulation is perceived by the participants, could the observations be a result of a conscious change of pressure distributed across the foot? It is also incredibly hard to manufacture such insoles that can reliably present vibration at a constant level due to the changes in pressure experienced throughout the gait cycle. It is therefore mechanically very difficult to provide effective, controlled stimulation during behaviours such as walking, where the forces change continuously throughout the step cycle. An alternative approach has been to provide texture to the sole of the foot to provide passive tactile stimulation.

5.4.2 Textured insoles

Similar to the application of vibration to the foot, as introduced briefly in Chapter 1, textured insoles have also been shown to reduce sway in the elderly (Palluel et al., 2008), and have even shown balance improvements in healthy populations (Kenny et al., 2019b; Park et al., 2023; Preszner-Domjan et al., 2012). This improvement is especially clear when the tactile system is up-weighted in the absence of visual information (Kenny et al., 2019b; Preszner-Domjan et al., 2012). Textured insoles also aim to make use of cutaneous reflexes, shown by the alteration in muscle activity recorded while walking (Curuk and Aruin, 2021; Kelleher et al., 2010; Nurse et al., 2005; Robb and Perry, 2022) and stepping onto a textured surface (Robb et al., 2021). Taken together, this once again demonstrates that simple additions to existing tactile feedback in the form of passive stimulation can be utilised to improve balance. In fact, the presence of a small boundary at the edge of the foot (Maki et al., 1999; Perry et al., 2008) can improve balance, or even the presence of a coin (Wang et al., 2016), causing localised elevated pressure to inform users of where pressure is currently distributed across the foot. Both of these interventions provide additional tactile feedback to alert users of small changes in pressure, and may aid in the activation of slowly adapting receptors do to their sensitivity to dynamic force. These also demonstrate the simplicity of the interventions that can be used to help prevent falls, and show the power of touch in balance maintenance.

5.4.3 Utilising touch to improve perceptions of stability

While textured insoles have shown promise, research has failed to investigate participant's perception of these insoles beyond assessing comfort, and the subsequent relationship to an individual's perception of their own stability and confidence in balance ability. An alternative approach would be to identify the textural property which may lead to improvements in balance performance, and therefore utilising conscious perceptual pathways to improve balance. In Chapter 4, hardness was the only significant contributor to participant's perception of stability, and roughness did not significantly contribute (Cleland et al., 2024), suggesting a new material property to focus on when creating insoles. This finding is in line with prior research that demonstrates poorer perceived stability when standing on foam (Anson et al., 2019), and an improvement in balance following hardness training (Morioka et al., 2009), both of which agree on importance of material hardness on balance. Moreover, a participant's conscious perception of stability is important, as shown by the positive relationship identified between subjective balance stability and confidence, and objective task performance (Castro et al., 2019; Schieppati et al., 1999). To make the most of this conscious perception, using tactile properties that aid one's perception of stability would be a powerful interventional approach that should be considered in future research.

5.5 Suggestions for future research

The importance of touch is multi-functional, impacting on balance via numerous pathways. Considering the novel findings presented within this thesis, together with existing knowledge presented within this discussion, there are many important research questions that can be proposed.

When considering how the foot acts with the environment, contact areas are much larger than the hand, and more practically, larger than the stimulation probes used within neurophysiological research. Yet, how cutaneous afferents respond to such large areas of stimulation is unknown. By using larger stimulation probes, the effects of skin stretch over a single receptive field will be reduced, with pressure applied more evenly across the foot. Moreover, the magnitudes of stimulation may activate afferents with receptive fields centimeters from the site of stimulation. Through the systematic increasing of distance from the centre of a single receptive field, it will be possible to identify the effects of the magnitude of stimulation and how skin mechanics support, or limit, signal propagation across the foot.

Secondly, shear forces should be investigated in greater detail. What is the magnitude of shear during a step? Are shear forces experienced during standing, and if so, how does this differ to those experienced during a step? How do patterns of shear across the foot differ depending on the region of the foot? Following the full characterisation of shear forces, the next step is to apply controlled shear to the foot sole, while recording from the peripheral nerve, to identify cutaneous responses to shear. The result of this research could further our understanding of cutaneous feedback during naturalistic stimulation.

Thirdly, further investigations of changes to the input to, and output from, the tactile system in ageing and diseased populations should be investigated. Section 5.3 detailed numerous changes that are observed, however, they have typically been from two different perspectives separately: biomechanical research has focused on changes in pressure and biomechanics, and sensory research has investigated alterations in perceptual and mechanical thresholds. However, as often, research includes participants that have already been diagnosed with sensory deficits, there is a large window of time between initial difficulties and research participation. If individuals were tracked more regularly, then it may be possible to further tease out the relationship between, for example, changes in sensation and ulceration in diabetic populations. Does the reduction in sensation lead to changes in the biomechanics and thus ulceration, or do the changes in biomechanics themselves preceded the reduction in sensation?

A fourth suggestion for future research relates to improving balance. Given that slowly adapting afferents respond more strongly to dynamic changes in pressure under high load, interventions that focus on activating this class of afferents preferentially should be trialled. Further investigation of how textured insoles are perceived could also provide an alternative route for improving balance using conscious perception.

5.6 Conclusion

Throughout this thesis, the role of touch in balance and gait has been investigated. The tactile system receives inputs that are spatially complex, in addition to the high forces that the rest of the human body does not experience, which must be considered by the tactile system. Regarding the high forces experienced during gait, slowly adapting afferents respond favourably while fast adapting receptors are not as sensitive to force. However, both slowly and fast adapting afferents are very sensitive to changes in stimulation. The tactile system also demonstrates a remarkable ability to maintain its perception despite the high forces experienced by the foot. Overall, tactile processing is able to provide essential information about the environment in which humans are standing or walking upon, providing essential input to the balance control feedback loop to contribute to fall prevention.

Chapter 6

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