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Cortical processing of Light Touch for the control of postural stability

David Kaulmann

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Dissertation

Chair of Movement Science

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Technical University of Munich

David Kaulmann

Devotement

Für meinen Vater der die Freude an Sport in mir erweckt hat. Danke, dass du immer mit mir trainiert hast.

Für meine Mutter, die mir die Freude am Lernen beigebracht hat. Danke, dass du so viel Geduld mit mir hattest.

Ohne eure Unterstützung und Liebe wäre ich niemals so weit gekommen.

For my Wife, who was always there when I needed a few words to keep me going. Thank you for being in my life and sharing the path with me.

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Introduction

“Use it or lose it” is a common saying among sport therapists. It describes the concept that body functions or systems deteriorate over time if a person does not use them. If one does not use a specific muscle, for example due to a cast, this muscle will lose its strength. This is why it is important to stay active. My grandmother used to cook long into her old age and tried to stay on her feet, managing the household as best as she still could. However, one day she tripped lightly. She had no possibility to recover her balance and she fell down the stairs. By a miracle, the worst injury was a broken toe. However, this incident was enough and from this day on, she was afraid to cook, to clean or even to walk. She did not want to fall ever again. She became sedentary and week by week, I had to observe how her muscles, her coordination, even her mental state deteriorated. Elderly people, as well as patients with neurological handicaps often face problems maintaining a quite stance, increasing their instability, which often leaves them incapable of reacting to disturbances. This naturally leads to increased falls risks, which can result in serious injuries and even death. The WHO estimates that annually 37.7 million falls are severe enough to require medical attention and 646.000 are actually fatal, making it the second leading cause of unintentional injury death world wide (WHO, 2018).

These numbers show how urgent fall prevention in these populations is. Of course, there are already aids to stabilize people during standing and walking such as wheeled walkers or even electric scooters. A wheeled walker has the advantage that it has storage space for groceries and can even be utilized as a seat, if a person needs a rest. In that sense, they are useful for elderly people, who otherwise would need to rely on external help. However, there are restrictions to their usefulness. Especially indoors, the use of these wheeled walkers is very limited. Homes of many people are not built like pension homes with wide hallways. They have nooks and crannies everywhere and occasionally a stairway needs to be climbed. If anything, they might even hinder a normal navigation through the house. Another disadvantage lies in the concept of these walking aids. The way people use them is by shifting their main weight forward from the own legs onto the aid. By doing so, they change the way they walk and thus change the demands of the lower leg muscles. This might lead to altered coordination patterns, with new ones emerging to fit the new way of walking, but losing the ones for unaided walking. Given a situation where a walking aid cannot be used a small misstep might be enough to trigger a fall, due to the person’s loss of the proper fall prevention strategy. A better way to manage fall prevention would be a technique that stabilizes balance impaired people but at the same time challenges them enough to prevent coordination from deteriorating. Using light fingertip contact with an earth fixed reference point does exactly that. It leads to stabilization of balance, but people have to do the work, straining the body systems enough so they do not lose their function. This phenomenon of light haptic contact is also referred to as Light Touch. Even though the effects of light touch have been shown in multiple studies, the underlying mechanisms are yet not completely understood. Especially the role of the higher brain functions leaves many questions open. To deal with this gab in the research my dissertation investigates the cortical correlates of light touch for the stabilization of balance.

To address this research question, the dissertation is structured as follows. The first chapter deals with the theoretical background underlying the research topic. It will describe the fundamentals of balance and postural control and what mechanism, including strategies and feedback loops exist to ensure stability of one’s posture. Afterwards, in the same chapter higher order brain functions of postural control are discussed and which areas and network are involved. The last part of the first chapter addresses the phenomenon of Light Touch. A definition of light touch will be given. Additionally, the known working mechanism, as well as effects are explained. The second chapter will explain the methods used to answer the related research questions. Following that the third chapter delves into the experimental work even further, including a summary of every publication, followed by the full manuscript of the publication. The last chapter will then provide an overarching discussion and put the results into context to the current state of research. Finally, in this context the postulated research question will be answered.

1 Theoretical Background

This chapter explains the fundamentals underlying the research question. First of all, the meaning of balance and postural control, as well as their differences are identified. Furthermore, it is explained how postural control is organized. In this regard, it is also discussed which higher brain functions, and which cortical areas are involved in the process of maintaining balance. The last part deals with light touch and its effects in general and for specific populations.

1.1 Postural control

The term Postural control generally describes the control of the body's position in space in order to maintain stability and orientation (Shumway-Cook & Woollacott, 2012). The fundamental purpose of postural control is to prevent the body from losing its balance and as an ultimate consequence falling over. In this context, postural orientation is defined as the ability to maintain an appropriate relationship between the body segments, and between the body and the environment for a task (Horak & Macpherson, 1996). On the other hand, postural stability, which is commonly known as balance, means that the Center of Mass (CoM) must be kept in the body's Boundary of Support (BoS). The BoS is dependent on the stance, as well as on other task constraints, e.g. reaching for an object. As long as the CoM does not leave the BoS stance is secured (Shumway-Cook & Woollacot, 2012). In order to ensure that the CoM stays within the BoS the Central Nervous System (CNS) generates forces to control motion. These forces are represented by the Centre of Pressure (CoP), which is the total force applied to the support surface. The CoP continuously moves around the CoM to keep the CoM within the BoS (Winter et al., 1990), which results in a constant sway movement of the body. This constant sway additionally serves as a constant feedback loop, augmenting the perception of the body's orientation in space, which leads to a more precise estimate of the current stability state.

Postural control is required for every task of the human body. However, depending on the task or the environment, such as reaching for an object, standing up or compensating perturbations, postural stability and postural orientation demands change (Horak & Macphearson, 1996). Independent form the task demands the CNS utilizes multiple subsystems to ensure postural control. These subsystems include musculoskeletal components, internal representations, adaptive mechanisms, anticipatory mechanisms, sensory strategies, individual sensory systems and neuromuscular synergies (Shumway-Cook & Woollacot, 2012). Due to the differences in task demands, the next chapters will look at these subsystems only in the context of maintaining quite stance.

Musculoskeletal components during quite stance include body alignment, muscle tone and postural tone. Muscle tone is the force with which a muscle resists being lengthen, or in other words its stiffness (Basmajian & Deluca, 1985). Biomechanical properties of the tendons and muscles provide inherent stiffness constraints that already help stabilize standing balance. However, these passive constraints are not enough to stabilize the body on its own. Previous studies by Winter et al. (1998) and Morasso & Schieppati (1999) calculated that around 200% of gravitational toppling torque is required to stabilize postural sway and prevent the body from losing balance. Sakanaka et al. (2016) calculated passive stiffness ranging between of 31% to 78%. This is in line with other studies calculating passive stiffness up to 91% toppling torque (Loram & Lakie, 2002). These results provide evidence that passive stiffness alone is not able to stabilize standing balance. Furthermore, this leads to the assumption that there is active modulation involved in the production of postural stiffness. Postural tone on the other hand are forces produced by postural muscles to counteract the force of gravity (Shumway-Cook & Woollacot, 2012). Essential for the postural tone are inputs from the sensory systems. As lesion studies have shown, lesions to the dorsal roots of the spinal cord reduce postural tone, indicating the importance of somatosensory inputs (Shumway-Cook & Woollacot, 2012). These inputs are provided by the visual, proprioception and vestibular system. Vision is the most prominent system used for balance control. Being able to see the body's alignment and relation to other object in space helps to maintain a quite stance. Visual inputs consist of foveal and peripheral information. Research suggests that the stimuli from the peripheral view is more important (Paillard, 1987). The vestibular system is situated in the inner ear and provides information about rotations and accelerations. Proprioception provides information of the joints and the position of limbs to one another, giving the CNS more information about the body's alignment. The last one primarily concerns detection of pressure under the soles of the feet. This helps to provide information about postural sway and the behavior of the center of pressure.

The importance of sensory information for postural control makes correct integration, interpretation and organization of this information critical. There are two theories how the CNS organizes sensory inputs. Stoffregen and Riccio (1988) postulated the intermodal theory of sensory organization. They proposed that the interaction of sensory inputs is based on lawful relationships, which they called invariants. All senses contribute information that is equally important for the stabilization of posture. In this model, sensory conflict does not exist but all information equally increases specificity in control and perception (Stoffregen & Riccio, 1988). Contradictory the intermodal theory of sensory organization is the "Sensory Weighting Hypothesis". It postulates that the relative weight given to a sense can be reweighted depending on the specifications of age, task and environment (Shumway-Cook & Woollacot, 2012). As a sensory input cue becomes either more or less accurate and unreliable for postural control it is given more or less weight. For example, if people have to stand in a dark room vision becomes less reliable and as such will be weights less, while somatosensory information from the sole of the feet are weights higher, in order to control posture correctly (Shumway-Cook & Woollacot, 2012).

During quite stance, two control modes are present to maintain equilibrium in different situations. These modes are feedforward and feedback control. Feedback control is used when sensory cues inform about a perturbation. Either in response to external perturbation to the support surface, or during trips and slips. Feedforward control is used for anticipatory postural adjustments, such as shifts of the CoM in preparation of a reaching movement, or during voluntary shifts of the CoM. Independently from control mode compensation strategies are used depending on the perturbation. Small perturbation or shifts of the CoM are usually compensated using the ankle strategy. To ensure equilibrium the body movement is primarily centered around the ankles. The gastrocnemius produces plantarflexion torque that first slows down and then revers the body's forwards motion. The Hamstrings and paraspinal muscles keep the knees and hips in an extended position (Shumway-Cook & Woollacot, 2012). With slightly large and faster perturbations, the torque produced by the ankle muscles is not enough to compensate shifts of the CoM, or when the support surface is compliant or smaller than the feet, the hip strategy is used to restore posture (Horak & Nashner, 1986). As a response, the hip joint produces large motions with antiphase rotations of the ankles. It should be noted that movement strategies are not strictly separated but range from a purely ankle to ankle plus hip strategy. (Shumway-Cook & Woollacot, 2012). In cases when in-place strategies, namely ankle and hip strategy, fail to compensate perturbations the stepping strategy is used. Interestingly, the stepping strategy is not just used when the CoM leaves its BoS, but even when the CoM is safely in its BoS (McIlroy & Maki, 1993). It is possible that these strategies are also dependent on the constraints of the task and that stepping is a preferred solution, unless task constraints dictate otherwise.

1.2 Higher order control of posture

The aforementioned compensation strategies, as well as anticipatory postural adjustments are not simply based on biomechanical properties or stretch reflexes, but are also influenced by central organization of posture.

1.2.1 Central organization of posture

The first indication of higher order control of posture can be derived from the flexibility of postural reactions. As studies of Macpherson (1991), and Horak & Macphearson (1996) demonstrated, postural reactions as an answer to external perturbations are greatly flexible (Massion et al., 2004). Depending on task constraints and conditions, the same external stimulus can result in different postural reactions. Usually perturbations to quite stance result in the main involvement of the leg muscles. However, if an additional support, such as a handrail, is available participants will grasp it and mainly use their arm muscles to ensure stability (Nashner & McCollum, 1985). These reactions contain proprioceptive reflex organization (Stuart, 2002), and are thus part of a higher level of control, responsible for selecting appropriate reflex actions (Massion et al., 2004). The second indicator is the existence of the aforementioned anticipatory postural adjustments. The nature of anticipation implies that there is a prediction of a forthcoming event, such as a perturbation. Predictions however, can only be made if a preexisting model exist. This model is developed from previous experience and learning and incorporates the external world, biomechanical properties and their interactions (Massion et al., 2004). Such a mesmerized representation of one’s body or internal model can only exist on a higher cortical level. Higher and lower order control do not exist separate from each other but are both necessary for the stabilization of posture. The “hierarchical model of posture” incorporates both functions and is derived from Bernstein’s “analogues model of movement organization” (Massion et al., 2004). The model assumes that two processes exist in the CNS that control posture. On the one side, a higher order one, which is responsible for the internal model, also called body schema. On the other hand, the lower order process, which control kinematics and kinetics, required for implementing postural functions (Massion et al., 2004). Given that higher order control is involved for the control of posture, it becomes necessary to identify which cortical areas are part of this higher order control.

1.2.2 Cortical involvement of postural control

Different cortical areas have been identified playing a role in the control of balance, mainly the Primary Motor Cortex, the sensorimotor cortex and the posterior parietal cortex. For example, The Primary Motor Cortex is responsible in the regulation of evoked postural responses in the lower limb (Taube et al., 2006). Taube et al. (2006) applied a single pulse TMS paradigm to demonstrate that corticospinal projection to the soleus muscle facilitates the long-latency responses of the muscle following abrupt backward translations of the support. Similarly, the sensorimotor cortex has been reported to play a role in not only the integration and in processing of sensory information, but also in adjusting the central set to modify externally triggered postural responses (Jacobs et al., 2008). Involvement of the Supplementary Motor Cortex has been found in motor planning and preparation for an adequate response to perturbations (Mihara et al., 2008; Maki & McIlroy, 2007; Fujimoto et al., 2014). Region of the cerebral cortex are also involved in the processing and integration of the sensory information coming from the fingertips when utilizing Light Touch for postural control. Ishigaki et al. (2016) provided evidence for the involvement of the left primary sensorimotor cortex and the left posterior parietal cortex in stance control with light tactile feedback. Johannsen et al. (2014) investigated how rTMS over the left inferior parietal gyrus (IPG) influences the integration of light fingertip contact for the control of postural sway. They found that rTMS over the left IPG reduced overshoot of sway after contact removal, which indicates that this brain region may play a role in sensory re-organization for sway control with contralateral fingertip contact.

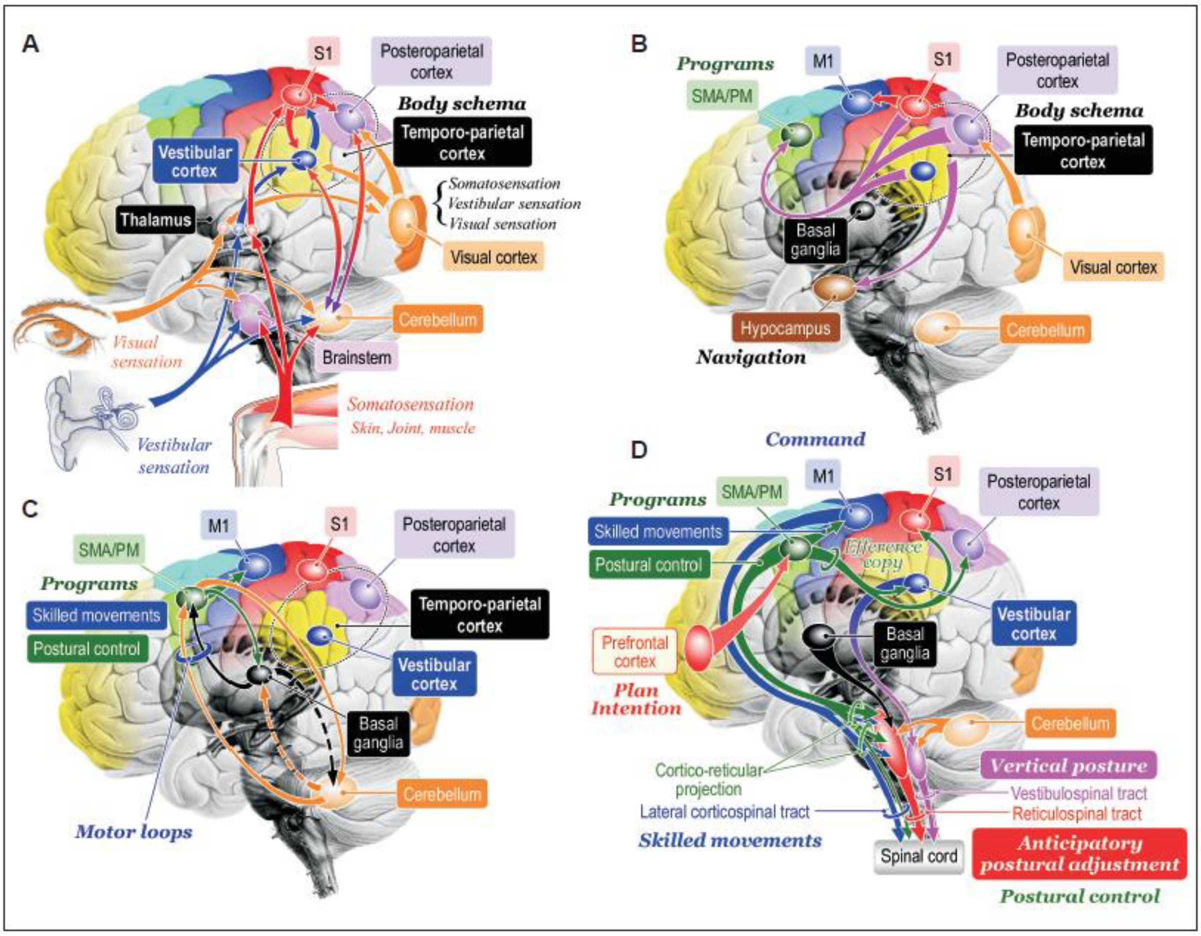

Figure 1. Cortical Involvement during postural control (Takakusaki, 2017)

Figure 1. shows the involvement of the cortical areas for the control of posture. At first the cognition of the bodily information, which were described in the previous chapter. Sensory signals from the vestibular, somatosensory and visual system converge to the brainstem, cerebellum, and thalamus. Visual information is further processed in the visual cortex. Likewise, vestibular input, as well as information from the sensorimotor system are processed in their respective cortical areas, the vestibular cortex and sensory motor cortex (S1) (Takakusaki, 2017). These signals are integrated into an internal model or body schema. This process is likely at the temporoparietal cortex, including the vestibular cortex and posterior parietal cortex. Following the cognition and integration of the sensory information, they are then transmitted to the supplementary motor area (SMA) and premotor area (PM), in order to produce motor programs. Similarly, the information is transferred to hippocampus and is used to navigate further behaviors (Takakusaki, 2017). In order to execute a meaningful, goal directed response a motor program has to be constructed. The motor cortex, in cooperation with the basal ganglia, as well as the cerebellum generates these motor programs (Takakusaki, 2017). Signals from the prefrontal cortex, including plans and intentions may trigger to run

motor programs in the SMA/PM, which may include those for purposeful movements and associating postural control. They are send to the M1 so that goal-directed purposeful skilled movements can be executed. On the other hand, the postural control program may be utilized to generate anticipatory postural adjustment via cortico-reticular and reticulospinal tract (Takakusaki, 2017).

Several studies implied a role of cortical neural circuits in the control of posture when anticipating a perturbation to body balance. Mochizuki et al. (2008) investigated cortical activity in preparation and reaction to full body perturbations. Cortical activity of 15 subjects was monitored during self-initiated, as well as unpredictable mechanical perturbations. Participants stood on a force plate, wearing a harness around the sternum. In the self-initiated perturbation condition, participants held a wireless computer mouse in their right hand and decided for themselves when the load would be released. In the unpredictable perturbation condition, release of the load occurred at random times. Results show that cortical activity in the preparation period was not associated with the motor act of perturbation initiation and was dissociable from cortical activity related to anticipatory postural muscle activation. In unpredictable trials, preparation activity was absent. The peak amplitude and latency of the N1 potential after perturbation was initiated were larger and later than for predictable trials. The authors concluded that self-initiated postural instability evokes cortical activity prior to and following perturbation onset. Pre-perturbation cortical activity is associated with changing central set to modulate appropriate perturbation-evoked balance responses (Mochizuki et al. 2008). In a following study, Mochizuki et al. (2009) investigated whether there a difference between self-initiated and externally initiated perturbations in terms of cortical activity. Participants were tested in three perturbation conditions: cued external perturbations, cued self-initiated perturbations and un-cued self-initiated perturbations. Results show no differences in pre-perturbation cortical activity across tasks. N1 potentials in the time after perturbation were significantly larger in external perturbations that were cued, compared to both the self-initiated cued perturbation and no cued self-initiated perturbations. No differences in muscle activity or CoP excursion amplitude was found. Using mechanisms that are different in nature but initiate temporal predictable perturbations, cortical events with similar spatio-temporal and magnitude are evoked. This shows that even though cues that inform about the onset of postural instability can be different they evoke consistent cortical processing. These results taken together show cortical potentials preceding self-initiated perturbations, as well as predictable external perturbations, highlighting differences in amplitude and temporal characteristics. These cortical activities might represent adjustments in a central set prior to the onset of a known perturbation (Mochizuki et al., 2008). Depending on alterations in the cognitive state, such as changes in the cognitive load or attentional focus, initial sensory-motor conditions, prior experience and prior warning of a perturbation influences the central set (Jacobs & Horak, 2007).

1.3 Light Touch

As mentioned earlier the CNS uses different sensory systems to help control balance. These systems are vision, the vestibular system, proprioception and somatosensory. Vision is the most prominent system used for balance control. Being able to see the body's alignment and relation to other object in space helps to maintain a quite upright stance. The vestibular system is situated in the inner ear and provides information about rotations and accelerations. Proprioception provides information of the joints and the position of limbs to one another, giving the CNS more information about the body's alignment. The last one primarily concerns detection of pressure under the soles of the feet. This helps to provide information about postural sway and the behavior of the center of pressure. However, the versatility of the CNS allows it to use other information channels, as long as they carry body sway relevant information. One of these other channels can be light haptic fingertip contact, also called "Light Touch" (LT) to detect and optimize postural sway. Light Touch is usually associated with a contacting force of 1N, which is established with an earth fixed referent point. Jeka et al. (1997) investigated the differences of touch forces for the stabilization of balance. Participants had to maintain either no contact, light contact with a contact force up to 1N or force contact, which allowed them to touch the reference point as strong as desired. Trials were performed with eyes or open and eyes closed. They found that medio-lateral sway was highest in the eyes closed-no contact condition and was reduced in all other conditions. Interestingly light touch and force touch lowered sway equivalently, in both eyes closed and eyes open conditions (Jeka et al. 1997). 1N of contact force is not enough to provide mechanical support. Somatosensory receptors of the skin detect shear force changes that are produced by small sway patterns. These changes together with proprioceptive information provide additional information about the body's orientation in space, reducing uncertainties and decreasing postural sway.

However, this is an oversimplification of the working mechanism of Light touch. In order to further elucidate these working mechanisms the next chapter will describe them in more detail.

1.3.1 Effects of Light Touch

Since the discovery of the light touch phenomenon many studies could reproduce this solid effect and even extend it to other populations. First of all, Holden et al. (1994) were able to show that lightly touching a stable surface improves postural sway in healthy participants. These results have been further confirmed by Jeka & Lackner (1994). In their study participants stood in Tandem-Romberg on a force plate, with either eyes closed or eyes open. Three touch condition were tested: no contact, light touch (~1N) and force touch (as much force as desired). Results revealed that light touch was not only as effective as force touch, but also as effective as vision. These results highlight the effectiveness of light haptic contact. This becomes even more obvious when looking at the versatility of light touch. Krishnamoorthy et al. (2002) were able to show that light touch is not limited by actively establishing it, but that participants also benefit when light touch is being applied passively. In their study Krishnamoorthy et al. investigated differences of touch locations, as well as active touch and fixation of the finger to an external reference point. Results show that passive contact at the head or neck can be more effective for stabilizing postural sway. Furthermore, sway seemed to be reduced even more if the finger was fixed to the reference point, compared to freely touching it. Important to know is that the net forces of the fixation were still less than 1N, meaning it was still not providing mechanical support (Krishnamoorthy et al., 2002). In the same study Krishnamoorthy et al. performed a second experiment in which they investigated whether the contact point need to be earth fixed or not. Participants were instructed to either hold a weight of 3kg in front of them or via a pulley system. Additionally, participants established or removed fingertip contact to a touch pad with their left hand. Results show a reduction of postural sway while holding a load suspended using a pulley system. They assume that he system of postural stabilization can use either of the two sensory inputs to reduce postural sway, as long as they carry body sway related information. In this case one provides a fixed reference point in space, and the other force changes at the point of contact related to the sway (Krishnamoorthy et al., 2002).

The potential of light touch for sensorial supplementation for sway control has been shown in several populations with balance impairment as well (Baldan et al., 2014). Tremblay et al (2004) compared healthy young and adults and elderly people and whether there are differences in utilizing light touch for balance control. Results show what elderly people used lightly more force when establishing touch, which was accounted for a compensation strategy for a decrease of tactile sensitivity. However, touch force was still around 1.21N only and did not result in mechanical support. Nevertheless, elderly people were able to utilize light touch and decreased their sway variability. In another study carried out by Baccini et al. (2007) results reveal an even higher effectiveness of light touch for decreasing postural sway in elderly people. They also compared young healthy adults to healthy elders and could show that elderlies were able to decrease their sway even more. Another population that suffers from decreased sensitivity are patients with diabetic peripheral neuropathy. These patients suffer from somatosensory loss in their feet, limiting the sensory input for balance control. Dickstein et al. (2003) investigated if patients with peripheral neuropathy are able to utilize Light Touch, in order to improve balance control. They tested healthy subjects and patients on two two surfaces (firm or foam) with eyes open or closed, establishing either light touch, heavy touch or no touch. Results show that patients with somatosensory loss were able to utilize light touch. Effects of light and heavy touch were similar in the somatosensory loss and control groups and a reduction of postural sway could be observed after application of light touch (Dickstein et al., 2003). As mention before the vestibular system contributes to the control of posture as well. Thus patients with vestibular loss often suffer from imbalances. Lackner et al. (1999) wanted to test whether patients with bilateral vestibular loss would profit from light haptic contact and be able to balance as well as normal subjects in the dark without finger contact. Subjects stood in Tandem Romberg in a dark room with either eyes open or eyes closed. Three touch conditions were tested: no touch, light touch and unrestricted force touch. Without contact, none of the vestibular loss subjects could stand for more than a few seconds in the dark without falling. However, with light touch patients improved their stability and were even better than healthy controls in the dark without light touch. Additionally, patients swayed less in the dark with light touch than with eyes open without touch, and less with eyes open and touch than just sight. These results signify the effectiveness of light touch. It seems that during quiet stance light touch can be as effective or even more so than vestibular function for minimizing postural sway (Lackner et al., 1999). Another patient population facing problems with impaired balance control leading to increased fall risk are people diagnosed with Parkinson’s disease. However, patients with Parkinson’s disease suffer from degraded proprioception, which might limit the application of light touch. Rabin et al. (2013) followed up on the question whether patients with Parkinson’s disease can use light touch to improve their stability. Patients and healthy controls were again tested with no touch, light touch and unrestricted force touch, with and without vision. Results show that indeed patients were able to utilize light touch. They swayed more than healthy control, but were still able to reduce sway when using non-supportive light contact, and even showed better effects than vision alone (Rabin et al., 2013). Also in patients with multiple sclerosis balance control is often diminished which leads to an impairment in many daily activities and increases their fall risk. In a study by Kanekar et al. (2013) they investigated if patients with Multiple Sclerosis benefit from Light Touch for balance control. Participants were instructed to stand on a force plate either with their eyes open or closed. The two conditions touch and no touch were tested. First of all, patients with multiple sclerosis showed significant postural instability in the absence vision. However, after initiating light touch postural sway was reduced in all conditions and can be considered a useful balance rehabilitative strategy (Kanekar et al., 2013).

In addition to sway control in quite stance, the postural control system is also concerned with maintaining balance in dynamic situations, such as when compensating an either foreseeable or unpredictable external perturbation. Johannsen et al. (2007), show that light touch results in faster stabilization and reduced body sway following both externally and self-imposed body balance perturbations. They investigated the effects of shoulder light touch on sway variability during balance perturbations induced by either pulling on or being pulled by a hand held device. Body sway was greater with light touch in the case of voluntary pull but no difference was found directly after reflex pull. In the time course after perturbation light touch resulted in significantly lower sway variability and a faster stabilization. They assume that shoulder light touch contact only affects immediate postural responses to voluntary pull but improves later postural responses in both perturbation conditions. A study by Martinelli could also show the benefits of light touch on postural responses following perturbations. Imposing the sudden release of a backward load to the trunk, Martinelli et al. (2015) reported that light touch reduced and slowed displacement of the CoP as well as decreased activity in the lower limbs’ Gastrocnemius muscle with greater effects in more challenging sensory conditions. They investigated the effects of light touch on postural responses under different visual and support surface conditions, analyzing different epochs ranging from the pre-perturbation period to recovery. Results revealed that light touch modulates the postural response in all epochs associated with an unanticipated mechanical perturbation. Muscle activity was reduced in all epochs, while CoP displacement showed more prominent effects in conditions manipulating sensory information relevant for balance control. Finally, Johannsen and co-workers (2017) provided evidence for the benefit of light touch in dynamic postural contexts by exerting abrupt backward perturbations onto participants standing on a compliant springboard under different conditions of visual feedback. Participants stood on a compliant springboard and had to compensate for mechanical induced perturbations. Additionally, visual inputs were altered, showing either no visual environment, a static environment or a dynamic visual environment of swaying branches. The utilization of light touch stabilized balance and decreased thigh muscle activity by up to 30%, which indicates that light touch optimizes mechanical and metabolic costs of balance compensation following a perturbation (Johannsen et al., 2017).

1.3.2 Working mechanisms of Light Touch

In order for the information received by light touch to be used it has to be integrated and incorporated with the other body sway related information. In a study by Bolton et al. (2011) they compared cortical sensory excitability between tasks with and without light touch while standing. They performed two experiments. In the first experiment, median nerve stimulation of the touch hand resulted in the facilitation of the P50, N140, and P200 compared to when the hand was not contacting a surface. In the second experiment subjects maintained light touch with either an earth fixed reference point or a touch reference that was attached to their wrist. Thus this reference point did not provide sway related information. P50 and N140 modulation was no longer present in either touch condition, leading them to suggest that previously observed changes might result from attention to light touch. However, P200 was facilitated for stable touch over wrist reference touch. They interpret this as task-specific regulation of the cortical representation of the afferent input form the fingertip, if they carry body sway related information. In their study Franzen et al. (2011) looked at changes of axial postural tone through the application of light touch. They found that axial postural tone can be modulated by light touch and that increased postural hip tone is associated with decreased sway. More interestingly, they postulate that changes in subjects' perception from trunk to surface rotation when changing from no touch to haptic touch, suggests that the postural control system switches from a global to a local trunk-centred reference frame after light touch has been integrated. A study by Ishigaki et al. (2016) shed light onto the cortical activity during light haptic contact. They could show increased high-alpha TRPD in the left primary sensorimotor cortex area and left posterior parietal cortex area, when light touch was established. Further involvement of the posterior parietal cortex has been shown by Azanon et al. (2010). Regions within the posterior parietal cortices are likely to be involved in the remapping of somatosensory and proprioceptive information into a body-centred frames of reference. Another way gathering insight into the cortical activity of light touch and its working mechanism is using TMS. In healthy participants cortical areas are facilitated or inhibited, depending on the protocol, to see how this effects behaviour. Johannsen et al. (2014) used repetitive transcranial magnetic stimulation (rTMS) to see how this affects light touch integration. They applied rTMS of 1 Hz for 20 minutes over the left hemisphere inferior parietal gyrus (IPG) as well as middle frontal gyrus (MFG). Sway was assessed before and after stimulation. During quite stance participants performed 6 onset and offset transition of light touch. They observed a short overshoot of sway after contact onset as well as after removal, with a higher overshoot after finger contact removal. Even tough steady state sway was not affected by rTMS, they found a reduced overshoot of sway after stimulation of the IPG.

Another explanation for the working mechanism was proposed by Stoffregen et al. (2000). Suprapostural tasks are those tasks where stabilizing posture is not a goal in itself, but is controlled in order to fulfill another task goal, e.g. reading a sign board. In their study Stoffregen et al. placed participants in front of a visual target and varied target distance, as well as visual task. Visual Targets were either near or far. The visual task was either staring at a blank target, or counting the frequency of letters in a block or text (visual search task). Results reveal that sway variability was reduced when the target was nearer or when performing the visual search task. They assume that the visual search task introduced more constraints on the visual system and that postural sway was reduced to improve visual performance. So far is has been shown that a vision dependent task goal, e.g. reading a sign, can lead to a reduction of sway, in order to enhance task performance. It is possible to assume that a haptic dependent task goal, such as staying only in light contact with a reference point also represents a suprapostural task, which leads to a decrease of sway variability, in order to minimize shear forces and force variability at the contact point. Riley et al. (1999) tested whether there are differences of light touch depending on the instructions. Participants stood with eyes closed and established light touch with an adjacent pliable surface. One group was only instructed to establish light touch while the other group was in instructed to keep the contact to a minimum. Only in the group where contact had to be kept at a minimum postural sway was reduced. This study gives evidence to the assumption that light touch may also serve as a suprapostural task.

It is plausible to assume that both working mechanism contribute to the effect of light haptic contact on balance control. Even though the working mechanisms of light touch are not yet entirely understood, the positive benefits of light touch have been observed in many studies, with different populations.

2 Methods

2.1 Postural sway analysis

In order to assess body sway, participants were required in all four experiments to stand in Tandem-Romberg stance on a force plate (Bertec FP4060-10, Columbus, Ohio, USA), recording ground reaction forces at 600Hz. CoP data of the force plate was digitally low-pass filtered with a cut-off frequency of 10 Hz (dual-pass, 4th-order Butterworth). CoP position was differentiated to obtain CoP rate-of-change in m/s(dCoP). The sway time series was segmented in to temporal bins of 500ms duration. The standard deviation (SD) of anteroposterior (AP) and medio-lateral (ML) dCoP was extracted for each bin.

In the third study additional to CoP rate-of-change, sway complexity was calculated. I used Detrended Fluctuation Analysis, in order to characterize the fluctuation dynamics of body sway in non-transitory, steady postural states. Segments of 5 s duration centered in between contact events were extracted from the time series of CoP position and appended in order to create time series of at least 25s. DFA scaling exponent α as the slope of the linear regression of the log-log scaled detrended fluctuation parameter as a function of the temporal window width was obtained.

In order to characterize balance recovery in the fourth study, I followed a similar approach as applied in Johannsen et al. [4]. The standard deviation of the medio-lateral dCoP (SD dCoP) was calculated for 13 temporal bins of 1 s duration before and after the moment of the perturbation. The 3 time bins before perturbation were used as baseline sway. Across the 10 bins after perturbation, an exponential decreasing non-linear regression $x(t) = C + A^{*}e^{\left(-\frac{t}{B}\right)}$ was calculated, yielding the function parameters A (intercept), B (time constant) and C (asymptote). The intercept is derived from the body sway at perturbation (t=0) and therefore reflects the immediate effect of the perturbation. The time constant represents the rate of stabilization of body sway after the perturbation with shorter time constants indicating faster stabilization. The asymptote, indicates the level of steady-state long-term stabilization (steady-state sway).

2.2 Finger Force Analysis

Light Touch is defined as haptic contact around 1N applied force to the contact reference. In order to control for the correct amount of applied force, participants were required to apply fingertip contact with a force torque transducer (6DoF Nano 17 force-torque transducer; ATI Industrial Automation, Apex, USA). Vertical force was recorded with 200Hz. Data was then low-pass filtered using a Butterworth filter and afterwards interpolated to 600Hz to match with data recorded form the force plate.

In the first and third study onset and removal time point of each touch period was determined. For the first study contact durations were then additionally sorted into the following categories: T1 (0.8 s – 1.6 s) and T2 (2.0 s – 2.6 s) as short duration conditions and T10 (8.0 s – 13.0 s) and T20 (18.0 s – 22.0 s) as the long duration conditions. Trial segments with other contact durations were discarded.

2.3 Kinematic Analysis

Body kinematics were recorded using 4 infrared motion capture cameras (Qualisys, Göteborg, Sweden) at 120Hz. A whole body model was used with reflective markers placed at the contacting fingertip, wrist, shoulders, C7, T5, Sternum, hip, ankle and head. However, data was only recorded and was not processed further or used in the later data analysis.

2.4 EMG Analysis

Surface EMG (1kHz) of the Gastrocnemius, Soleus and Tibialis Anterior of the posterior supporting leg was recorded to measure muscle activity (Trigno Wireless PM-W05, Delsys, Natic, MA, USA). EMG data was band-pass filtered between 10 and 500 Hz, rectified and smoothed by a moving average with 15ms width to obtain the EMG activity envelope of a muscle. For each muscle peak amplitude and the area-under-the-curve was extracted. Peak amplitude served as indicator for phasic activity directly following a perturbation, while the area-under-the-curve indicated general muscle activity.

2.5 Continuous Theta Burst Stimulation

Continuous Theta Burst Stimulation (cTBS) of an intensity of 80% of the passive motor threshold for 60 seconds was applied over the right or left Posterior Parietal Cortex with a TMS coil (PMD70-pCool; MAG & More, Munich, Germany). Stimulation effects are usually lasting between 20 minutes and 1 hour (Staines & Bolton, 2013). Sham stimulation was applied over the same target locations as for the cTBS using a sham coil (PMD70-pCool-Sham; MAG & More, Munich, Germany) with the same intensity. Sham coils do not produce a focused magnetic field, leading to no known cortical activity changes, but induce similar clicking sounds and sensation of the scalp. The passive motor threshold was determined by registering the motor evoked potential (MEP) at the musculi interossei dorsales manus of the left hand following a single TMS pulse over the hand representation of the right-hemisphere primary motor cortex. A staircase procedure was used to adjust the pulse intensity until a 50µV MEP could be elicited reliably (Siebner & Zimmermann, 2007).

High-resolution anatomical brain scans were acquired before the study at the University Hospital Großhadern, Center for Sensorimotor Research and consisted of a T1 MPRAGE (3T whole-body scanner, Sigma HDx, GE Healthcare, Milwaukee, Wisconsin, USA).

In order to define the cTBS target area, I used MNI coordinates (x = 26, y =258, z = 43) reported in Azañón et al. (2010). Stimulating in this target area cTBS should have disrupted activity in the Superior Parietal Lobule (SPL; Area 7A) and Intraparietal Sulcus (IPS). Stimulation locations were targeted using real-time neuronavigation software (TMS Neuronavigator, Brain Innovation, Maastricht, Netherlands). In order to localize the stimulation area for each individual participant, the high-resolution scan was co-registered and normalized to the MNI template.

2.6 Visual Signal Detection Task (VSDT)

The second study utilized a visual signal detection task in order to provide an additional task goal other than remaining in quite stance, in order to identify possible effects of suprapostural tasks on balance control. The difficulty in this task was implicitly coupled to either body sway directly or to the contact force during fingertip light touch. A single Landolt-C served as the visual target, randomly changing the direction of its opening every 2 s while continuously oscillating horizontally at 0.09 Hz across the entire width of the display.

Participants had to press a button with their non-dominant hand as fast as possible when the opening of the Landolt-C pointed upwards. Depending on the implicit performance of body sway or contact force of the finger the Landolt-C additionally jittered horizontally. Body sway was assessed in four IFC conditions: (1) LT with independent jitter (LT-IJ), (2) LT with jitter depending on LT contact force (LT-CF), (3) LT with jitter depending on body sway (LT-BS), and (4) no contact with jitter depending on body sway (NT-BS).

2.7 Perturbation paradigm

In the fourth study I implemented a perturbation paradigm using a robotic arm. During every single trial, a robotic arm (KUKA LBR4+, Augsburg, Germany) pushed participants at their right shoulder in medio-lateral direction. The force of a lateral push was exerted with either 1%, 4% or 7% of their respective body weight in a randomized order in a block consisting of 6 trials with 2 trials for each force. Using a percentage of the body weight for every single participant, results in different absolute forces for the participants.

3 Publications

3.1 Summary of study I

Light touch is often not established in a constant way, but actually used in intermittent time periods, for example while moving down the aisle of a moving train. However, not many studies have addressed the course of sway stabilization before and after light touch initiation. In the first publication I investigated the effects of intermittent light touch and whether there are differences arising from handedness. Twelve healthy, right-handed young adults stood in normal bipedal stance with eyes closed on a force plate with an earth-fixed reference directly in front. On hearing a high-pitched tone, participants initiated light finger contact while on a low–pitched tone, participants removed light fingertip contact. The testing protocol consisted of 2 blocks of at least 6 trials, with every trial containing four active transitions between No-touch and Touch (“onset”) and Touch and No-touch (“removal”). Active contact durations were 1s, 1.5s, 10s and 20s in randomized order. Every No-contact interval was at least 10 seconds long. Onset and removal of time points were randomized, resulting in total trial durations of at least 130s. First if all results showed that there was no difference between the dominant or non-dominant hand in terms of sway reduction. Light touch with either hand resulted on the same amount of reduction. However, there was a difference between hands regarding the return-to-baseline sway after contact removal, with a more persistent after effect when using the dominant hand. Regarding contact durations, actively removing intermittent light touch at the fingertip leads to a rapid increase in sway within 500 ms after contact removal for contact durations shorter than 2.5 seconds irrespective of the contacting hand. In contrast, longer contact durations, especially with the dominant hand results in greater after effects, with a delayed return-to-baseline sway. In conclusion, the results provide evidence that light touch is affected by hemispheric lateralization. While the dominant hand showed a delayed return-to-baseline effect after long contact durations, it was not observed when the non-dominant hand was used for contact. This difference cannot be explained by differences in the tactile sensitivity of the contacting index fingers of the two hands. It seems more likely that these differences are due to faster consolidation of a postural set utilizing light touch, when this tactile feedback is processed in the dominant hemisphere.

Contributions:

Experimental conceptualization was designed by the mentor Leif Johannsen. Data collection was carried out by David Kaulmann and Leif Johannsen. Data and statistical analysis was carried out by David Kaulmann, under the supervision of Leif Johannsen. The manuscript for the publication was written by David Kaulmann, with Leif Johannsen providing feedback and corrections.

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The international scientific journal IEEE gave permission to use the publication for this dissertation.

Consolidation of the postural set during voluntary intermittent light finger contact as a function of hand dominance

David Kaulmann[1], Hui-Ya Chen[2], Leif Johannsen[1,3]
[1]Human Movement Science, Department of Sport and Health Sciences, Technische Universität München, Germany
[2]School of Physical Therapy, Chung Shan Medical University, Taichung, Taiwan
[3]School of Health Sciences, Faculty of Medicine and Health Sciences, University of East Anglia, Norwich, United Kingdom

Abstract— **Light fingertip contact with an earth-fixed referent decreases body sway. In a previous study Johannsen et al. (2014) demonstrated longer return-to-baseline of body sway for intermittent contacts of more than 2 seconds duration. This indicates that sway reduction with light tactile contact involves postural control strategies independent of the availability of tactile feedback and may depend on the intention to control body sway with light touch feedback. In the present study, we investigated the effect of hand dominance on post-contact return-to-baseline to probe for potential inter-hemispheric differences in the utilization of light finger contact for sway control. Twelve healthy, right-handed young adults stood in normal bipedal stance with eyes closed on a force plate with an earth-fixed referent directly in front. Acoustic signals instructed onset and removal of intermittent light touch. We found that return-to-baseline of sway following longer contact durations is affected by hand dominance with the dominant hand resulting in a slower return to No-contact levels of sway. Our results indicate that the light touch postural set is more persistent and might need longer to disengage when established with the dominant hand or takes longer to consolidate when established with the non-dominant hand.**

I. INTRODUCTION

In daily life, we often establish intermittent haptic contact with objects in our environment to orientate ourselves and to yield stability of body balance. For example, walking down the aisle on a moving train carriage, we move from handhold to handhold prepared to counter any unexpected perturbations. Or when we cross an unlighted room, we haptically move from contact to contact to gain an estimate of our position and to augment our sense of spatial orientation.

Light fingertip contact with an earth-fixed reference leads to a reduction in body sway [1]. Only a few studies have addressed the time course of sway before and after a contact transition [2, 3, 4]. Sway stabilization with light touch is a time-consuming integrative and attention demanding process [2, 3, 5].

In terms of a multimodal sensory strategy, it seems rather costly if the postural control system switches between different multisensory sets each time intermittent contact is established or removed [6]. Instead, while anticipating upcoming contact intervals and thus the imminent availability of reliable haptic feedback, keeping a multisensory set including the haptic channel temporarily active might offer an advantage with respect to the costs of switching the postural sets [7]. For example, Bove and colleagues (2006) demonstrated that the intention to establish contact within less than 5 seconds leads to reductions in body sway before contact is established. Schiepatti and colleagues [8] proposed that transient anticipatory processes are involved in the preparation of the central postural set to the context of stance control with light contact. Investigating intermittent touch with only short contact durations, Johannsen et al. (2014) demonstrated that contact durations of more than 2 s result in slower recovery of reduced sway to baseline levels after contact removal. These observations indicate that the integration of fingertip contact requires no less than about 2 seconds and is likely to involve not only bottom-up sensory processing but also top-down, “intentional” control of body sway and tactile attention.

The two hemispheres of the human brain might play different roles in the control of body sway with and without light touch [9, 10]. In the present study we not only aimed to replicate previous findings with intermittent but longer contact durations, we also intended to probe for differences between the dominant and non-dominant hemispheres regarding their influence on switching the postural set in right-handed participants during phases of intermittent light touch.

II. METHODS

Participants

Twelve healthy young adults (mean age = 25.8, SD = 2.6; 7 woman and 5 men) were recruited for the current study. Inclusion criteria were (1) right hand dominance and (2) no balance impairment. All participants were informed about the study protocol and signed a written informed consent was provided. The study was approved by the Clinical Research Ethics committee of the Technical University of Munich.

Procedure

Participants stood barefoot in normal bipedal stance. After the height of the stand was adjusted to each participant’s waist level, participants were asked to hold their index finger of the dominant hand above a touch plate while keeping the outstretched arm in a comfortable posture. We instructed participants to close their eyes, and to stand relaxed but as still as possible without speaking.

Trials were started when participants indicated that they were ready. On hearing a high-pitched tone, participants flexed their index finger at the metacarpal-phalangeal joint to initiate light finger contact. On a low–pitched tone, participants lifted their index finger just above the touch plate. Before testing participants could practice the task in order to familiarize themselves with the experimental protocol. Afterwards they performed at least 6 trials with 30 s break in between hands.

After participants finished sway testing, we assessed the tactile discrimination threshold of each hand's index fingertip using 13 orientation gratings with a gap width ranging from 0.35 mm to 5.50 mm [11]. Participants had to judge whether gratings were aligned straight or orthogonal with the fingertip. Gratings were applied manually for about two seconds. Testing protocol consisted of a staircase procedure which ended either after ten successful reversals or a total of 50 grating presentations. The final tactile acuity threshold was derived from the average of the last 10 presentations.

Apparatus

A force plate (600 Hz; Bertec FP4060-10, USA) measured the six components of the ground reaction forces and moments to determine the antero-posterior (COP_{ap}) and medio-lateral (COP_{ml}) components of Centre-of-Pressure. In response to a high-pitched or low-pitched auditory cue, participants either made or withdrew fingertip contact with a touch plate (3 cm diameter), mounted on a stand at waist level to the front of the participants. A force-torque transducer (ATI Nano17, USA) measured the normal and horizontal shear forces applied to the touch plate with a rate of 200 Hz. We measured body kinematics (60 Hz; Zebris, Germany) in terms of trunk motion with three acoustic markers placed at wrist, shoulder and hip.

Each balance testing consisted of 2 blocks of at least 6 trials per hand (range=6 to 8 trials; blocked, randomized order: dominant hand, non-dominant hand). Every balance trial contained four auditorily triggered active transitions between No-touch and Touch ("onset") and Touch and No-touch ("removal"). The acoustically cued intermittent active contact durations were 1 s, 1.5 s, 10 s and 20 s in randomized order. Every No-contact interval was at least 10 seconds long. Onset and removal time points were randomized resulting in total trial durations of at least 130 s.

Data reduction and statistical analysis

All data were interpolated to 600 Hz and merged before low-pass filtering with a fourth-order Butterworth filter (10 Hz cut-off frequency) and differentiated to yield rate of change. According to the vertical touch force as detected by the force-torque sensor, onset and removal time points of each touch period were determined. For comparisons between contact durations participants' *actual* contact durations were sorted into the following categories: T1 (0.8 s – 1.6 s), T2 (2.0 s – 2.6 s), T10 (8.0 s – 13.0 s) and T20 (18.0 s – 22.0 s). Trial segments with other contact durations were discarded. Subsequently, the T1 and T2 categories were averaged and subsumed under "short" duration conditions, while T10 and T20 were averaged and combined as "long" contact durations for statistical analysis.

Non-discarded trial segments were divided into bins of 500 ms duration from 5 s before to 5 s after a contact transition. Sway within each bin was quantified in terms of the standard deviation (SD) of the Centre-of-Pressure velocity in the anterior-posterior ($dCOP_{ap}$) direction. Sway parameters were averaged for each duration condition of all trials a participant performed.

Using SPSS 18.0 software (Chicago, IL, USA), repeated-measures ANOVAs were performed with time course across a range of 500 ms bins, contact duration and contacting hand as within-subject factors.

In order to characterise the return of sway to the No-contact baseline following contact removal, we fitted linear regressions across three time bins: 0.5 s before removal, 0.5 s and 1 s after removal. Statistical analysis of regression slope and zero-offset was conducted with repeated-measures ANOVAs with contact duration and contacting hand as within-subject factors. Level of significance was set to p=.05 after Greenhouse-Geisser correction. Effects with estimated effects sizes of partial $\eta^2>0.14$ were considered large.

III. RESULTS

Statistical analysis of the tactile discrimination thresholds revealed no significant differences between the dominant and non-dominant hands (p = 0.33), which suggests that hand dominance did not influence tactile sensitivity of the respective hand. Figure 1 shows the tactile sensitivity thresholds for the index finger of both hands.

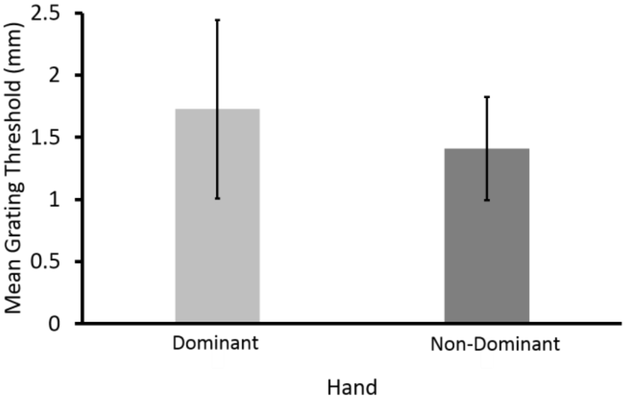

Figure 1. Tactile sensitivity threshold in terms of the just noticeable gap width for the dominant (light grey) and non-dominant (dark grey) hand. Error bars indicate standard error of the mean.

Figure 2 shows average sway progression from 5 s before to 5 s after contact onset and Figure 3 shows average sway progression around contact removal for short (upper panel) and long (lower panel) contact durations. Sway is oscillating close to the No-contact baseline before contact is established. After the onset of touch, sway transiently rises above and then begins to drop below the baseline. Similarly, sway with light touch is noticeably below the baseline before contact is removed. Following contact removal, sway once again overshoots the No-contact baseline and then settles towards it.

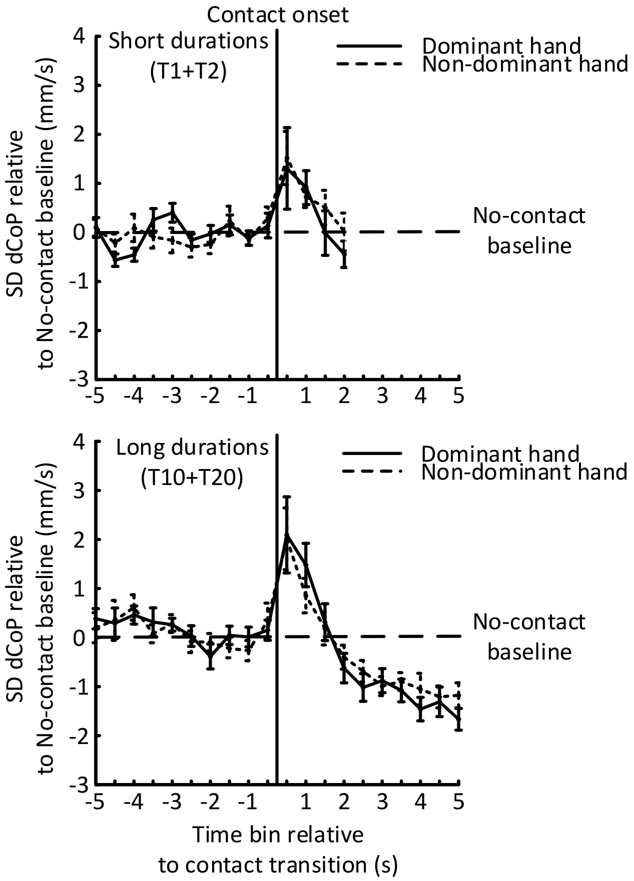

Figure 2. Average time course of sway across 500 ms bins from 5 s before to 5 s after contact onset for the short durations (upper panel) and long durations (lower panel) for the dominant (bold line) and non-dominant hand (dashed line). Error bars indicate standard error of the mean.

Although steady-state sway with light touch of the dominant hand (time bins from 5 s to .5s before contact removal) appears lower compared to the non-dominant hand, the two contact conditions were statistically not different (p>.25, partial η^2=.12).

The increase in sway after removal of long duration light touch appears less rapid with the dominant hand compared to the non-dominant hand. In order to assess the return-to-baseline of sway after contact removal (including the overshoot), we examined the time course of sway during the removal transitions. Focussing on the range from 0.5 seconds before to 1.5 seconds after. We found statistical significant interactions of between hand and contact duration (F(1,11)=6.83, p=.02, partial η^2=.38) as well as between hand, contact duration and time course (F(3,33)= 4.18, p=.03, partial η^2=.28). Post-hoc single comparisons showed a strong difference between the dominant and non-dominant hand at the 0.5 s time bin after long duration contact removal (F(1,11)=3.47, p=.08, partial η^2=.24) with lower sway after contact removal of dominant hand.

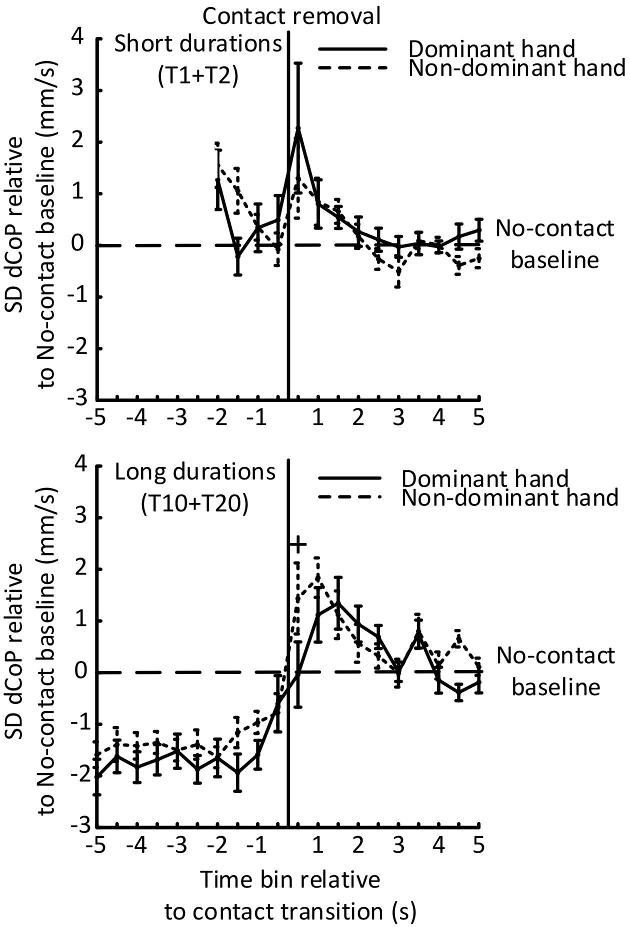

Figure 3. Average time course of sway across 500 ms bins from 5 s before to 5 s after contact removal for the short durations (upper panel) and long durations (lower panel) for the dominant (bold line) and non-dominant hand (dashed line). Error bars indicate standard error of the mean. The cross indicated the tendency of a difference between both hands (p>.1).

Sway overshoot after removal of the non-dominant hand had progressed further during this period, almost reaching peak overshoot, compared to the dominant hand. Peak overshoot, although numerically lower following contact with the dominant hand, was not affected by limb dominance (….).

Analysis of the linear regression parameters showed significant interactions between contact durations and hand for the regression slope (F(1,11)=6.89, p=.02, partial η^2=.39) and offset (F(1,11)=6.70, p=.03, partial η^2=.38). For both slope and offset after short duration contact, post-hoc single comparisons did not show differences between hands. After long duration contact, however, previous contact with the dominant hand resulted in a lower slope (F(1,11)=5.55, p=.04, partial η^2=.34) and offset (F(1,11)=4.81, p=.05, partial η^2=.30) compared to the non-dominant hand. Figure 4 shows linear regression slope and offset of the sway progression following contact removal for short and long contact durations as a function of the hand tested.

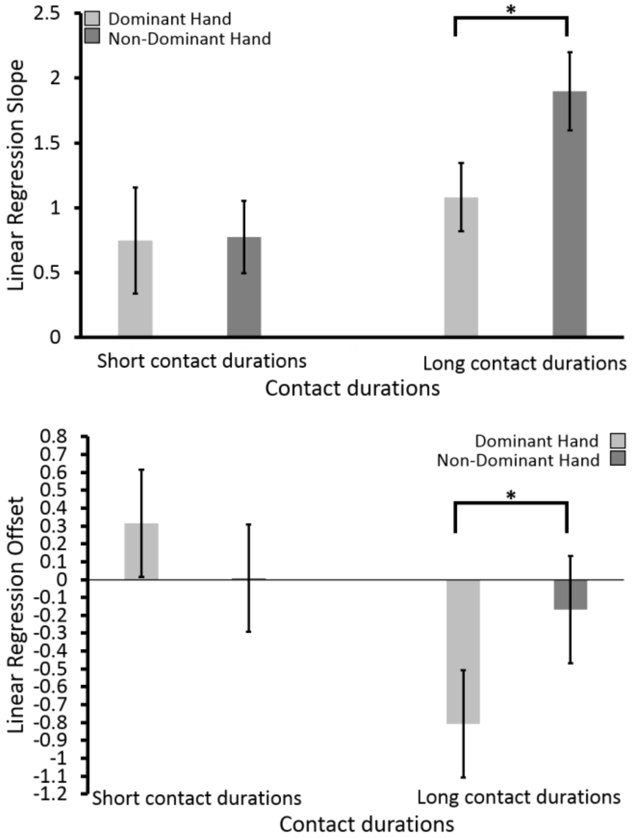

Figure 4. Linear regression slope (upper panel) and offset (lower panel) for short and long contact durations for the dominant (light grey bars) and non-dominant (dark grey bars) hand. Error bars indicate standard error of the mean. An asterisk indicates a significant comparison between hands ($p<0.05$).

IV. DISCUSSION

Actively removing intermittent light touch at the fingertip leads to a rapid increase in sway within 500 ms after contact removal for contact durations shorter than 2.5 seconds irrespective of the contacting hand. Similarly, contact at the fingertip of the non-dominant hand also shows rapid increase for longer durations. In contrast, more persistent contact with the dominant hand results in delayed sway return-to-baseline.

In our present study, the general progression of sway during a contact removal transition is in line with the previous study of Johannsen et al. [4]. They showed that short contact durations initiate a reduction in sway but do not result in a significant reduction. A delayed return-to-baseline only occurred for contact durations longer than 2 seconds. Contact durations longer than 5 seconds, however, were not tested. Therefore, our present study tested longer contact durations, which ought to more likely result in steady-state sway with light contact. Indeed, we found that the sway progression after touch removal increased at a lower rate but only when longer duration touch was established with the dominant hand. With the non-dominant hand, contact resulted in a rapid sway increase similar to the short contact durations.

A central question to be answered is whether the less rapid, more gradual return of sway to No-contact levels after removal of the dominant hand resembles a functional advantage or disadvantage? It could be that a rapid return expresses a fast readjustment in the multisensory strategy of the postural control system. The instantiation of a new postural set involving the haptic channel could result in inter-sensory conflict between an information-deprived haptic channel and the other senses. The sway overshoot observed could be a consequence of the sudden deprivation of a highly weighted tactile signal leading to acute intermodal conflict. For example, following abrupt cessation of long-term support surface sway referencing, Peterka and Loughlin demonstrated the emergence of transient, involuntary 1 Hz body oscillations, possibly due to over-corrective torque production [12].

It seems more reasonable to delay postural set switching until the likelihood is high that the haptic channel will provide reliable feedback for an extended period. Once such a steady state has been reached it also seems reasonable to keep this set active and delay disengagement, if further contact periods are expected to occur in the near future. This reasoning seems to apply to the pattern we observed for the dominant hand. As we tested right-handed participants it implies that the dominant left hemisphere is involved in this strategy. In a previous study, we observed that disruption of the left-hemisphere inferior parietal gyrus (IPG) by repetitive transcranial magnetic stimulation (rTMS) inhibited sway overshoot following unexpected, passive removal of light contact [4]. This could mean that the left IPG plays a role in the detection of multisensory conflict or the directing of tactile attention. This is in correspondence with reports by Ishigaki and colleagues [13], who suspected involvement of the left primary somatosensory and posterior parietal cortices in the processing and integration of steady-state right hand light touch. On the other hand, we disrupted the left and right PPC by cTBS and did not find any alterations in sway progression following removal of active light touch [10]. Nevertheless, all-in-all the evidence suggests that the left-hemisphere plays some role in the control of body sway with light haptic feedback form the contralateral, right hand, for example in the consolidation of an adequate central postural set.

Why did the non-dominant, left hand not demonstrate a delayed return-to-baseline similar to the dominant, right hand? One possibility is that consolidation of the central postural set for the light touch with the non-dominant hand has a longer time constant. For example, our participants might have been more used to explore the environment with their dominant hand.

An aftereffect on postural sway following an extended duration of lightly gripping a cane was reported by Oshita and Yano [14]. They investigated the effect of lightly touching a cane on postural sway and ankle- joint muscle activity. They found decreased sway and decreased co-contraction of the ankle joint muscles when the cane was gripped lightly. These reductions were also present after lifting off the cane from the ground. In interestingly, their participants used the left hand to grip the cane, presumably the non-dominant hand. Oshita and Yano did not assess varying contact durations but 30 s contact only. It seems that also light contact with the non-dominant hand can lead to slow return-to-baseline of body sway. Perhaps contact durations of more than 20 s duration are the prerequisite.

To conclude, the occurrence of a delayed return-to-baseline of sway following removal of fingertip light touch is affected by hemispheric lateralization. While the dominant hand showed a delayed return-to-baseline effect after long contact durations, it was not observed when the non-dominant hand was used for contact. This difference cannot be explained by differences in the tactile sensitivity of the contacting index fingers of the two hands. Instead, the effect could rely on a difference in the rate of consolidation of a light touch postural set, with faster consolidation when tactile feedback is processed in the dominant hemisphere.

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3.2 Summary of study II

The effects of Light Touch are often contributed to additional sensory information provided by the fingertip. However, some studies suggest that the additional sensory information isn't the only reason postural sway is decreased during light touch. Moreover, an individual's task goals are also taken into account. Riccio and Stoffregen found that body sway is also reduced when performing a visual task. In this situation body sway is decreased in order to make the goal of the visual task easier and more successful. Tasks that impose such task restrictions are also referred to as suprapostural tasks. Similarly, precision control of light touch with an earth-fixed reference, can also be considered a suprapostural task. In other words, sway is already proactively reduced before any sensory feedback modulates sway, in order to successfully fulfill the task goal of keeping only light fingertip contact. In this study the perceptual difficulty in a visual signal detection task (VSDT) was implicitly coupled (implicit feedback coupling, IFC) to either body sway directly or to the contact force during fingertip light touch. In both situations, it was expected that body sway would be reduced to ease the difficulty of the visual task. Ten healthy right-handed young adults faced a flat-screen display, while standing in tandem stance on a force plate. A single Landolt-C was presented as the VSDT target, randomly changing the direction of its opening every 2s while continuously oscillating horizontally (0.09 Hz) across the entire width of the display. Participants were instructed to press a response button with their non-dominant hand as fast as possible when the opening of the Landolt-C pointed upwards. Depending on the implicit performance of body sway or contact force of the finger the Landolt-C additionally jittered horizontally. This means that the VSDT became harder, when swaying greater on the force plate, or exerting too much force with the finger. On the other hand, the task became easier when fulfilling the implicit task goal more successfully, by maintaining a quite stance or light fingertip contact around 1N. Body sway was assessed in four IFC conditions: (1) LT with independent jitter (LT-IJ), (2) LT with jitter depending on LT contact force (LT-CF), (3) LT with jitter depending on body sway (LT-BS), and (4) no contact with jitter depending on body sway (NT-BS). IFC conditions were tested in randomly ordered blocks of five trials (120s duration). Results show a greater sway reduction in those conditions that had an implicit feedback coupling (LT-CF, LT-BS) compared to the LT condition alone. Interestingly, these results are direction specific with effects only in the medio-lateral direction. Both feedback loops (contact force and force plate coupling) during light touch minimized sway, which implies either that no control hierarchy existed for whole body sway and fingertip contact (integration of both control processes) or that the hierarchy can be switched flexibly (one facilitating the other), if it serves the implicit goal of reduced perceptual noise and enhanced performance for the visual task.

Contributions:

Experimental concept and set up was designed by David Kaulmann. Programming for the visual stimulus was done with the help of the student assistant Max Hünemörder. Participant acquisition and data collection was carried out by David Kaulmann, as well as data and statistical analysis using Matlab and R. The manuscript for the publication was written by David Kaulmann, with Leif Johannsen providing feedback and corrections.

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LETTER TO THE EDITORS

Serving performance in a suprapostural visual signal detection task: context-dependent and direction-specific control of body sway with fingertip light touch

David Kaulmann[1] · **Joachim Hermsdörfer**[1] · **Leif Johannsen**[1,2]

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Dear Sirs,

When upright stance body sway is increased during horizontal oscillatory smooth pursuit, it may indicate interference between oculomotor and sway control, potentially due to an efferent oculomotor signal [1]. In specific contexts, however, body sway reduction has also been reported during smooth pursuit [2]. Riccio and Stoffregen [3] argued that the postural control system also takes into account an individual's behavioural goals, such as performance in a "suprapostural" task, especially when the task imposes visual demands in contrast to cognitive demands [4]. Therefore, sway may be dampened proactively to reduce self-imposed variability and to improve oculomotor accuracy during visual tracking or reduce retinal slip in a visual discrimination task [2, 5, 6]. Similarly, precision control of fingertip light touch (LT) with an earth-fixed reference, which most reliably reduces body sway [7], has been considered a suprapostural task [8]. The interpretation of proactive sway control assisting fingertip LT is corroborated by observations that body sway may be reduced for intermittent periods when LT is absent, but nevertheless relevant to the postural context [9–11]. Is a natural sensorimotor congruency always required to elicit task-related sway adaptation or does it generalize to more complex sensorimotor stimulus–response mappings? Our present study adopted a "biofeedback" approach, in which the perceptual difficulty in a visual signal detection task (VSDT) was coupled (implicit feedback coupling, IFC) to either body sway directly or to the contact force during fingertip light touch. In both situations, we expected that body sway would be reduced proactively to ease the difficulty of the VSDT.

Ten healthy right-handed young adults (4 females, 6 males; age = 26.7 yrs, SD 6.0) faced a flat-screen display (Samsung UE40D6500) in tandem stance. A force plate (600 Hz; Bertec FP4060-10) recorded body sway in terms of centre-of-pressure (CoP) fluctuations. A single Landolt-C was presented as the VSDT target, randomly changing the direction of its opening every 2 s while continuously oscillating horizontally (0.09 Hz) across the entire width of the display. Participants were instructed to press a response button with their non-dominant hand as fast as possible when the opening of the Landolt-C pointed upwards. The dominant arm was held in a default elbow-flexed posture, enabling the extended index fingertip to contact a force–torque transducer (200 Hz; ATI Nano17) on a height-adjustable stand positioned in front. VSDT perceptual difficulty varied in terms of the amplitude of random vertical target jitter. Body sway was assessed in four IFC conditions: (1) LT with independent jitter (LT-IJ), (2) LT with jitter depending on LT contact force (LT-CF), (3) LT with jitter depending on body sway (LT-BS), and (4) no contact with jitter depending on body sway (NT-BS). IFC conditions were tested in randomly ordered blocks of five trials (120 s duration). Further details of the experimental setup are provided in the online methods supplements (Figs. 2 and 3). CoP was low-pass filtered (4th-order dual-pass Butterworth with 10 Hz cut-off) and differentiated to express body sway as the standard deviation of CoP velocity (dCoP). Repeated-measures

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✉ Leif Johannsen
L.Johannsen@uea.ac.uk

[1] Department of Sport and Health Sciences, Technical University Munich, Munich, Germany

[2] Faculty of Medicine and Health Sciences, School of Health Sciences, Queens Building, University of East Anglia, Norwich Research Park, Norwich NR4 7TJ, UK

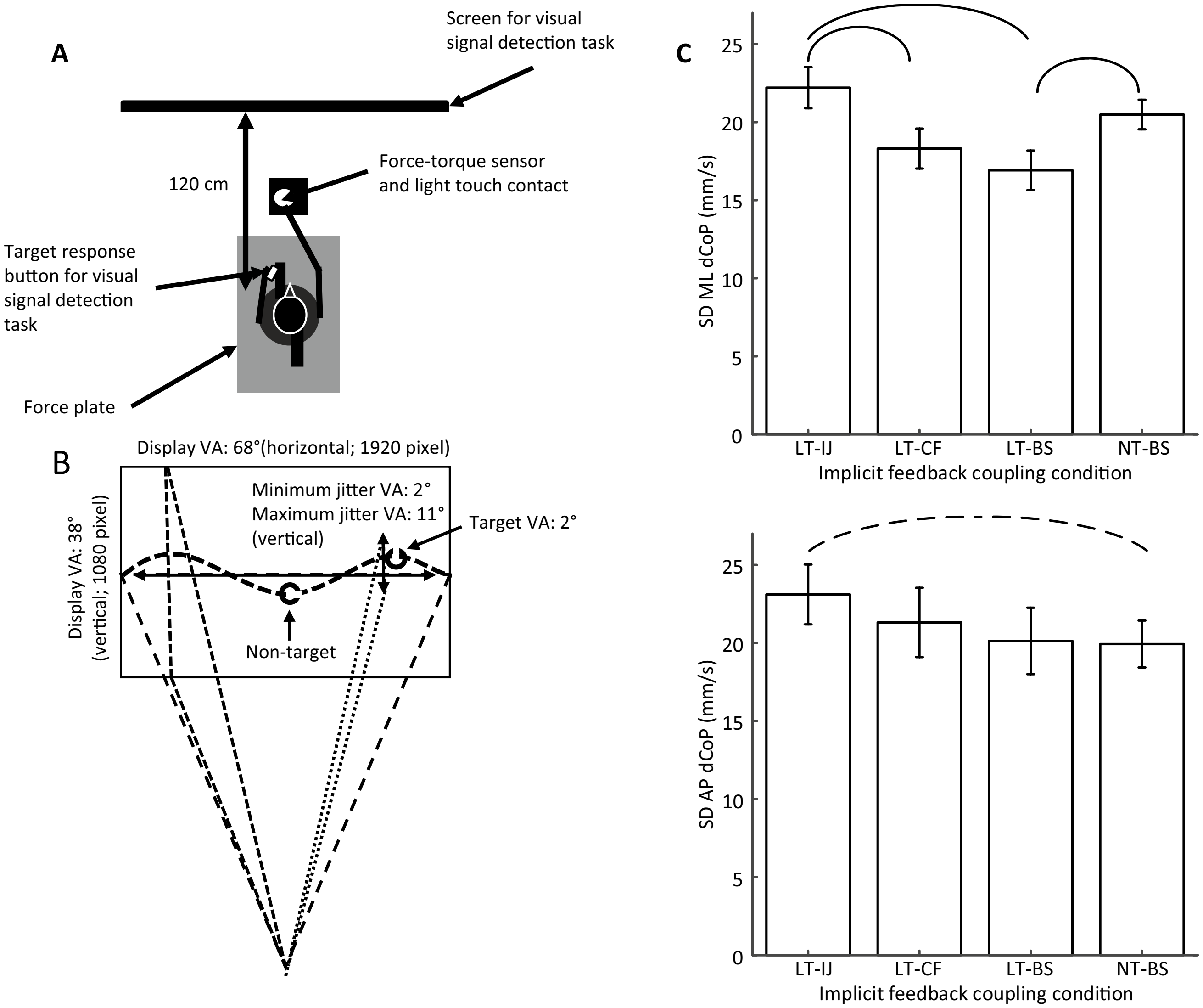

Fig. 1 **a** The experimental setup showing an individual in tandem stance on a force plate in front of the display screen with fingertip light touch of the dominant hand and a response button in the non-dominant hand. **b** Schematic of the stimulus display. A Landolt-C oscillated horizontally along a double sine-wave trajectory across the entire width of the display at a constant velocity of approximately 14°/s changing the direction of its opening every 2 s. Participants had to gaze track the target to press the response button when its opening pointed upwards. Random jitter of variable amplitude in the vertical direction disrupted the visibility of the Landolt-C opening, thereby affecting the difficulty of the visual signal detection task. Current jitter amplitude depended on the current fingertip contact force or current body sway. *VA* visual angle. **c** Variability of mediolateral (ML; upper panel) and anteroposterior (AP; lower panel) body sway velocity (SD dCoP) in each implicit feedback condition (IFC). LT-IJ: fingertip light touch with independent maximum jitter amplitude; LT-CF: jitter amplitude dependent on light touch fingertip contact force; LT-BS: jitter amplitude dependent on body sway with additional fingertip light touch; NT-BS: jitter amplitude dependent on body sway without additional fingertip light touch. Error bars indicate the standard error of the mean. Straight horizontal arcs indicate significant post hoc single comparisons ($p < 0.05$), and he dotted horizontal arc indicates a statistical tendency ($p < 0.10$)

ANOVA was calculated with IFC condition as within-subject factor. An alpha level of $p < 0.05$ was used after Greenhouse–Geisser correction. Post hoc single comparisons were Bonferroni-adjusted.

The proportion of hits in the VSDT task was 67% in LT-IJ, 80% in LT-CF, 77% in LT-BS, and 59% in NT-BS. Average LT force was 0.85 N (SD 0.17) with no difference between the IFC conditions with LT. Resulting body sway differed between the IFC conditions ($F(3,27) = 12.74$, $p < 0.001$; Fig. 1). Reduced mediolateral sway was found in both LT-CF and LT-BS compared to LT-IJ (both $p \leq 0.007$) and in LT-BS compared to NT-BS ($p = 0.003$). No difference between the IFC conditions was observed for anteroposterior sway ($p = 0.12$). Nevertheless, there was a tendency for a difference between LT-BS and LT-IJ ($p = 0.09$).

Our results demonstrate a direction-specific reduction in mediolateral body sway below a level achieved by LT sway-related feedback augmentation alone if an implicit feedback coupling is present. Similar direction-specificity of sway control has been reported in visuomanual aiming [12]. In visual search involving saccadic eye movements instead of smooth pursuit, Chen et al. [13] showed that LT improved search performance. Demands of the visual search task, however, reduced sway independent of LT availability so that two processes seemed to act in parallel [13]. Similarly, in our current study, both direct (LT-CF) and indirect (LT-BS) involvement of fingertip contact in an IFC condition minimized sway, which implies either that no control hierarchy existed for whole body sway and fingertip contact (integration of both control processes) or that the hierarchy can be reversed flexibly (one facilitating the other) if it serves the implicit goal of reduced perceptual noise and enhanced performance within the context of our suprapostural VSDT.

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Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflict of interest.

Ethical standards The study accorded to the ethical principles laid down in the 1964 Declaration of Helsinki and its later amendments and was approved by the Technical University of Munich Ethics Committee. All participants gave their informed consent prior to their inclusion in the study.

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3.3 Summary of study III

In order to utilize light touch for balance stabilization the CNS has to integrate the haptic signal from the fingertip into the body's own reference frame. One area that is likely involved in this process is the Posterior Parietal Cortex (PPC). In order to investigate the role of the PPC I implemented a TMS experiment, altering the activation of the PPC. It was expected that the disruption of the PPC would attenuate the effect of light touch on body sway. The experiment was divided into three sessions, one to acquire a brain scan for real-time neuronavigation and two experimental sessions. Each experimental session consisted of a balance pre-test, the application of TMS and a balance post-test. During the balance test participants stood blindfolded in Tandem-Romberg stance on a force plate, while initiating or removing fingertip contact following acoustic signals provided via headphones. Each balance testing consisted of 6 trials of at least 130 s duration with either the dominant or non-dominant hand. Each trial had six auditory triggered active transition between No-Touch and Touch ("onset") and Touch and No-Touch ("removal"). TMS consisted of continuous Theta Burst Stimulation (cTBS) of an intensity of 80% of the passive motor threshold for 60 seconds over the right or left PPC or a Sham stimulation. Against the hypothesis results revealed no effects of disruption of the left or right PPC for the integration of the haptic signal. Light Touch worked just as well after cTBS as it did following sham stimulation, decreasing sway variability. Interestingly, detrended fluctuation analysis (DFA) revealed an increase in sway complexity when light touch was utilized, compared to the no touch period. This provided evidence that the effects of light touch are not only limited to improvement of sway variability, but also improves sway complexity. Even more surprising was that following disruption of the right PPC we see a general reduction of sway variability, accompanied by a decrease of sway complexity. In contrast sham stimulation or cTBS over the left PPC showed no such general reduction. Decreased body way variability in combination with decreased sway complexity might be due to increased overall body stiffness, possibly resulting from less adaptability and in a reduced ability to compensate for unforeseen perturbations. This increased stiffness might be the result of reduced inhibition by a processes of active stability exploration.

Contributions:

The experiment was conceptualized by David Kaulmann, with feedback provided by Leif Johannsen Participant acquisition and data collection and TMS application was carried out by

David Kaulmann. Data and statistical analysis was also performed by David Kaulmann using Matlab and R. The manuscript for the publication was written by David Kaulmann, with Leif Johannsen and Joachim Hermsdörfer providing feedback and corrections.

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DR. LEIF JOHANNSEN (Orcid ID : 0000-0002-2441-3163)

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Disruption of right Posterior Parietal Cortex by cTBS alters the control of body balance in quiet stance

David Kaulmann[1], Joachim Hermsdörfer[1], Leif Johannsen[1,2]

[1]Human Movement Science, Department of Sport and Health Sciences, Technische Universität München, Germany

[2]School of Health Sciences, Faculty of Medicine and Health Sciences, University of East Anglia, Norwich, United Kingdom

Corresponding author:

Leif Johannsen

School of Health Sciences,
Faculty of Medicine and Health Sciences,
University of East Anglia,
Norwich Research Park,
Norwich, NR4 7TJ, United Kingdom

Email: L.Johannsen@uea.ac.uk

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Key words: cTBS, body sway control, light touch, posterior parietal cortex

Abstract

Control of body balance relies on the integration of multiple sensory modalities. Lightly touching an earth-fixed reference augments the control of body sway. We aimed to advance the understanding of cortical integration of an afferent signal from light fingertip contact (LT) for the stabilisation of standing body balance. Assuming that right-hemisphere Posterior Parietal Cortex (rPPC) is involved in the integration and processing of touch for postural control, we expected that disrupting rPPC would attenuate any effects of light touch. Eleven healthy right-handed young adults received continuous Theta Burst Stimulation over the left- and right-hemisphere PPC with sham stimulation as an additional control. Before and after stimulation, sway of the blindfolded participants was assessed in Tandem-Romberg stance with and without haptic contact. We analysed sway in terms of the variability of Centre-of-Pressure (CoP) rate of change as well as Detrended Fluctuation Analysis of CoP position. Light touch decreased sway variability in both directions but showed direction-specific changes in its dynamic complexity: a positive increase in complexity in the mediolateral direction coincided with a reduction in the anteroposterior direction. rPPC disruption affected the control of body sway in two ways: first, it led to an overall decrease in sway variability irrespective of the presence of LT; second, it reduced the complexity of sway with LT at the contralateral, non-dominant hand. We speculate that rPPC is involved in the active exploration of the postural stability state, with utilization of LT for this purpose if available, by normally inhibiting mechanisms of postural stiffness regulation.

Introduction

Keeping light contact ('light touch', LT) with objects in our environment augments the sensory feedback about the body's relative orientation in space and leads to reductions in body sway (Jeka & Lackner, 1994). In order to integrate haptic information from the fingertips into the postural control loop, the central nervous system (CNS) may require interpretation of a local contact signal within the context of the body's overall proprioceptive state. This includes both arm posture and stance configuration, which could involve transformations of the haptic signal into an egocentric reference frame.

The posterior parietal cortices may be central components of a distributed network of neural circuits for the processing of somatosensory and proprioceptive information in ego-centric frames of reference (Longo *et al.*, 2010; Medina & Coslett, 2010; Bolton, 2015). For example, Azañón et al. (2010) showed that disruption of the right posterior parietal cortex (rPPC) impairs conscious position judgements of tactile stimuli on the left forearm relative to the face. With respect to the processing of haptic information for the control of body sway, Franzen and colleagues (2011) suggested that the postural control system has switched from a global to a local trunk-centred reference frame after light touch has been integrated into the postural control loop. Thus, right-hemisphere PPC (rPPC) seems like a good candidate to test for involvement in the processing of a fingertip signal within an egocentric reference frame for the control of body sway.

Light touch of the dominant hand during quiet standing involves processing in the dominant left-hemisphere. Bolton *et al.* (2011) demonstrated that when the somatosensory feedback of the right hand contains sway-related information, brain activity at the left inferior parietal lobe caused by somatosensory-evoked potentials is modified by the specific postural context. In addition, Johannsen et al. (2015) investigated repetitive Transcranial Magnetic Stimulation (rTMS) over the left inferior parietal gyrus (IPG) to assess how stimulation affects the progression of sway before and after passive onset and removal of right-hand fingertip contact. They found that rTMS over the left IPG reduced overshoot of sway after contact removal, which indicates that this brain area may influence sensory reorganisation for sway control, for example in terms of directed tactile attention (Johannsen *et al.*, 2015). There is evidence, however, that regions exist also in the non-dominant, right hemisphere for the processing of ipsilateral touch in the context of upright stance. Bolton *et al.* (2012) reported that disruption of the right prefrontal cortex alters the processing of right hand somatosensory-evoked potentials during contact with an earth-fixed reference.

Nevertheless. in the two stimulation studies reviewed above steady-state sway with light touch was not affected, which raises the question if disruption of another region such as the PPC changes the light touch effect during steady-state sway and if the rPPC in particular is contributing to the processing of touch irrespective of the haptically stimulated body side. The aim of this study was therefore to investigate the involvement of cortical processes represented within both posterior parietal cortices in the processing of haptic afferents for the control of balance. Assuming similar asymmetries between the hemispheres in terms of the processing of tactile input within spatial reference frames, as observed with respect to the distribution of spatial attention (Azanon *et al.*, 2010) to the environment, we expected that disruption of the rPPC alters the integration of haptic afferences of both hands for sway control. In contrast, we expected that left-hemisphere PPC (lPPC) disruption would lead to an altered integration of touch of the contralateral hand only.

Methods

Participants

Eleven healthy right-handed young adults (mean age=25.45, SD 2.73; 6 women and 5 men) were recruited for the current study. Inclusion criteria were (1) right hand dominance, (2) no neurological or musculoskeletal disorders, (3) no balance impairment and (4) no reported cases of epilepsy. All participants were informed about the study protocol and signed a written informed consent. The study was approved by the Clinical Research Ethics committee of the Technical University of Munich.

Procedure

The experimental protocol was divided into three sessions. As a first session prior to the stimulation sessions a high resolution anatomical brain scan, consisting of a T1 MPRAGE (3T whole-body scanner, Signa HDx, GE Healthcare, Milwaukee, Wisconsin, USA) was carried out at the University Hospital Großhadern, Center for Sensorimotor Research. The brain scan was used in the following sessions for real-time neuronavigation in order to locate the respective stimulation area.

Each TMS session consisted of a balance pre-test, the application of TMS and a balance post-test. The balance tests required blindfolded participants to stand on a force plate (600Hz; Bertec FP4060-10, Columbus, Ohio, USA) in quiet Tandem-Romberg stance, while actively initiating and ceasing finger contact with an earth-fixed referent in response to an acoustic signal. The earth-fixed contact reference point was placed in front of the participants. They held one arm slightly angled in front of the body and reaching straight forward. The other arm remained passive with the hand touching the stomach in order to prevent subjects from using arm movement to correct their body balance. Each balance testing consisted of 6 trials of at least 130 seconds (blocked, randomized order: 3 with the dominant hand, 3 with the non-dominant hand). Durations of the single trials varied due to the randomization of the length of the interval between contact events. Tandem-Romberg stance posture was adjusted according to the contacting hand. When the dominant hand contacted the reference point, the leg on the same side took the rear tandem position. When the contacting hand changed, so did the position of the feet. Participants were instructed to stand relaxed and not flex their knees to lock legs in position.

Each balance trial had six auditory triggered active transitions between No-touch and Touch (lowering the finger to the contact; “onset”) and Touch and No-touch (raising the finger of the contact; “removal”). Every contact phase was at least 8 seconds long. Time points of contact onset and removal were randomized. We instructed participants to lightly press onto a contact plate downwards with a force around 1N. Before testing began, they practiced light touch in order to get a feeling for the applied force. Participants did not receive feedback about the contact force during a trial to avoid any attentional distractions and to prevent contacting from becoming an explicit precision task.

Body kinematics (4 Oqus 500 infrared cameras; 120 Hz; Qualisys, Göteborg, Sweden) and forces and torques at the reference contact location (6DoF Nano 17 force-torque transducer; 200 Hz; ATI Industrial Automation, Apex, USA) were assessed. To capture body motion, reflective markers were placed at contacting fingertip, wrist, shoulders, C7, Sternum, hip and ankle.

During the TMS we applied continuous Theta Burst Stimulation (cTBS) of an intensity of 80% of the passive motor threshold for 60 seconds over the rPPC or lPPC (Fig. 1a; PMD70-pCool; MAG & More, Munich, Germany). This protocol is widely used and stimulation effects can last from 20 minutes up to 1 hour (Staines & Bolton, 2013). A staircase procedure was used to determine the passive motor threshold. In order to define the cTBS target areas, we used the MNI coordinates reported in Azañón et al. (2010), who stimulated the right-hemisphere human homologue of macaque ventral intraparietal area. We therefore expected that cTBS would disrupt activity in the Superior Parietal Lobule (SPL; Area 7A) and Intraparietal Sulcus (IPS) of the respective hemisphere. Stimulation locations were targeted using real-time neuronavigation software (TMS Neuronavigator; Brain Innovation, Maastricht, The Netherlands). During stimulation participants were seated comfortably on a reclined chair facing a wall and keeping their head straight. Participants needed five steps from the seat to the force plate. They had to cover this distance with their eyes closed in order to preserve any aftereffect of the stimulation as best as possible.

Testing took place on two non-consecutive sessions with at least one day in between stimulation. The order of stimulation locations was randomized across participants with Sham stimulation being always the first stimulation in the second TMS-session. Sham stimulation was executed over the same target locations as for the cTBS (PMD70-pCool-Sham; MAG & More, Munich, Germany). The location alternated across the sequence of participants, so that odd and even numbered participants received lPPC or rPPC sham stimulation respectively. Six participants received a lPPC/rPPC order and five a rPPC/lPPC order of stimulation.

Data processing and statistical analysis

The data of the force-torque transducer as well as the kinematic motion capture system were interpolated to 600 Hz and merged with the force plate data. Data were digitally low-pass filtered with a cut-off frequency of 10 Hz (dual-pass, 4th-order Butterworth). Center-of-Pressure (CoP) position was differentiated to yield rate of change parameters (dCoP) in order to remove low frequency drift. Based on the Normal force detected by the force-torque sensor, the onset and offset timepoints of each touching period was determined. In order to represent the time course of sway from 5 s before to 5 s after a contact event (onset/offset), the sway time series was segmented in to temporal bins of 500ms duration. The standard deviation (SD) of anteroposterior (AP) and mediolateral (ML) dCoP was extracted for each bin. Data processing and extraction was conducted by MATLAB (MathWorks, 7.13 (2011b). Figure 1b shows the progression of contact force and sway velocity over one trial.

In order to characterize the fluctuation dynamics of body sway in non-transitory, steady postural states, segments of 5 s duration centered in between contact events were extracted from the time series of CoP position. These steady-state segments were appended in order to create time series of at least 25 s duration for Detrended Fluctuation Analysis (DFA) (Peng *et al.*, 1995; Amoud *et al.*, 2007; Duarte & Sternad, 2008). We followed the basic algorithm as described by Peng *et al.* (1995) and obtained the DFA scaling exponent α as the slope of the linear regression of the log-log scaled detrended fluctuation plot as a function of a temporal window width of up to 10 s duration.

Sway in the anteroposterior and mediolateral directions and the scaling exponents were statistically analysed using 4-factorial repeated-measures ANOVA with (1) contacting hand (dominant vs. non-dominant hand; ipsilateral vs. contralateral hand relative to stimulation side), (2) location of stimulation (rPPC, lPPC and Sham), (3) effect of stimulation (Pre- and Post-cTBS) and (4) time course for onset and offset events (time bins) as within-subject factors. In order to test for steady-state effects, time bins 4.5s to 3.5s before the contact event and the three last extracted time bins (4s to 5s) after the contact event were contrasted for both each respective event type. For statistical significance a Greenhouse-Geisser corrected p-value of smaller 0.05 was used. A similar analysis was conducted for the derived contact force. All statistical analyses were carried out using SPSS (IBM SPSS Statistics 21).

Results

Contacting force at the fingertip

Overall, average fingertip contacting force was 2.33 N. Statistical analysis of the average contacting force and its variability did not reveal any effect of hand dominance, location of stimulation, effect of stimulation or any interactions between these factors.

Variability of body sway during contact transitions

Figure 2 shows the progression of sway variability over the time course of 5 s before a contact transition to 5 s after in bins of 500 ms duration before and after cTBS for each of the three stimulation locations. Before onset of fingertip contact, sway variability of the mediolateral direction is high and drops gradually to a lower level after contact is initiated (F(19,190)=19.55, p<.001, η^2=.66). Sway variability remains low as long as contact is kept. Briefly after fingertip contact is removed, variability rises to higher, pre-contact levels (F(19,190)=40.18, p<.001, η^2=.80). A similar progression of sway can be observed in the anteroposterior direction (onset F(19,190)=16.83, p<.001, η^2=.63; offset F(19,190)=16.91, p<.001, η^2=.63).

In terms of the general effect of touch, comparisons between the time bins from 4.5s to 3.5s before a contact event and the three last extracted time bins after the same contact event revealed a reduction in body sway variability with touch by 21% in the mediolateral direction (onset: F(5,50)=36.96, p<.001, η^2=.79; removal: F(5,50)=122.49, p<.001, η^2=.93) and by 22% in the anteroposterior direction (onset: F(5,50)=56.12, p<.001, η^2=.85; removal: F(5,50)=51.87, p<.001, η^2=.84).

Regarding the effect of cTBS on sway variability, we found an interaction between stimulation location and stimulation effect in the mediolateral direction (F(2,20)=6.12, p=.02, η^2=.38). We performed post-hoc ANOVAs for each stimulation location and found general sway reductions after cTBS for both the onset (F(1,10)=5.14, p=.05, η^2=.34) and removal phases (F(1,10)=5.28, p=.04, η^2=.35) after rPPC stimulation but after either lPPC or sham stimulation. In the mediolateral direction, stimulation over the rPPC decreased the sway variability in all phases with and without fingertip contact by 8%. In contrast, sway variability was not reduced by lPPC (3% increase) or sham stimulation (1% increase). In the anteroposterior direction, a similar numerical trend could be observed (rPPC: 8% decrease; lPPC: 3% decrease; sham: 2% increase). However, the interaction between stimulation location and stimulation effect was not significant (F(2,20)=1.78, p=.20, η^2=.15). Figure 3 shows sway variability averaged across all time bins (both onset and removal transitions combined) as a function stimulation location and effect for the mediolateral (Fig. 3a) and the anteroposterior direction (Fig. 3b).

Sway fluctuation dynamics

Detrended fluctuation analysis of sway for the mediolateral direction revealed that fingertip touch decreased the scaling exponent α in the DFA plots compared to No-touch (Fig. 4a; F(1,10)=18.91, p<.001, η^2=.65). In contrast, the scaling exponent α increased with touch in the anteroposterior direction (F(1,10)=9.59, p=.01, η^2=.49).

Furthermore, we found a marginally significant 4-way interaction between touch, hand, stimulation location and stimulation effect in the mediolateral direction (F(2,20)=2.77, p=.10, η^2=.22). Post-hoc single comparisons expressed that rPPC stimulation increased the scaling exponent α with contact of the non-dominant hand (F(1,10)=6.06, p=.03, η^2=.38; Fig. 5b). In contrast, lPPC and sham stimulation resulted in no difference in this contact condition (Fig. 5a and Fig. 5c).

Discussion

We aimed evaluate the effects of disruption by cTBS of the PPC in both hemispheres on the processing of fingertip light touch for body sway control in Tandem Romberg stance. Surprisingly, after stimulation of the rPPC, the general level of sway variability was decreased. This encompassed all trial phases including those in which light fingertip contact was applied and body sway reduced by the augmented sensory feedback. Light touch changed the sway dynamics in a direction-specific manner in favour of the mediolateral direction. In the mediolateral direction, however, a second effect of rPPC disruption became visible. After the stimulation, the sway dynamics degraded in those phases in which light contact was kept with the non-dominant, contralateral hand.

The general reduction after rPPC disruption appears like an unexpected improvement in sway. Reduced sway variability, however, does not necessarily mean that individuals possess a greater degree of stability in terms of the ability to compensate a balance disturbance. For example, variability is adjusted by the postural control system according to the demands of a specific supra-postural task and seems to be necessary for flexible reactions to external perturbations (Balasubramaniam *et al.*, 2000). It can be argued that the reduction in sway reflects an unfavorable effect in terms of participants becoming less adaptive and less able to compensate for unexpected perturbations (Lipsitz, 2002) after rPPC disruption. Possibly, rPPC disruption resulted in an increase in overall postural stiffness by muscular co-contractions and therefore showed reduced body sway variability (Maurer & Peterka, 2005).

If disruption of the rPPC results in increased stiffness, then the question remains which functional aspect of body sway control the rPPC does represent? We like to propose a functional equilibrium between a process that controls body stiffness and a process that actively explores the own body's current state of stability in the context of the specific postural configuration and orientation (Riccio *et al.*, 1992). Control of stiffness plays a crucial part when interacting with the environment, for example to gain postural support or when anticipating external perturbations. In the absence of an external perturbation, active stability state exploration would probe for any deviation from the body's equilibrium point by registering the forces and torques required to counteract any environmental dynamics exerted onto the body. Possibly, the rPPC is involved in this active exploration process.

Yadav and Sainburg (2014) propose a distinction between two neural systems for limb control, one for predictive control of arm movements and the other for control of arm stiffness (impedance). The former system is attributed to the dominant (left) hemisphere in right-dominant participants, while the latter to the non-dominant (right) hemisphere (Yadav & Sainburg, 2014). Several studies in stroke patients have implied that the right hemisphere may dominate the control of body sway (Rode *et al.*, 1997; Peurala *et al.*, 2007; Tasseel-Ponche *et al.*, 2015). Assuming that stiffness control by the right hemisphere generalizes from the non-dominant arm to the control of body sway, our results suggest that stiffness control and active exploration are two processes coordinated within the right hemisphere. If the rPPC contributes to active exploration, the question remains, which right-hemisphere regions control stiffness. It is likely that the rPPC is part of a network, which is distributed across several brain regions responsible for maintaining a functional equilibrium (Bolton, 2015). Studies reveal a wide spread of different cortical areas involved in the control of balance ranging from the prefrontal cortex, primary motor cortex and the parietal cortex (Mihara et al. 2012) to the basal ganglia (Visser & Bloem, 2005). Functions of the basal ganglia include muscle tone regulation and control of automatic postural responses and patients with dysfunction in that area often show axial stiffness, gait freezing or co-contraction (Visser & Bloem, 2005). Thus, the basal ganglia seem like a good candidate to be involved in stiffness or impedance control. The prefrontal, primary motor and parietal cortices might form the exploratory processes for balance control.

Our results show reduced variability of sway with light touch in both directions. Although apparently a similar effect occurred in both directions, there might be differences between mediolateral and anteroposterior sway as the complexity measure of sway dynamics showed opposite changes for both directions. While the scaling exponent α decreases with light touch in the mediolateral direction, it rises in the anteroposterior direction (Fig. 4). In both directions the scaling exponent α was greater than 1, which is interpreted as a non-stationary signal with low long term self-similarity and reduced complexity. 1/f noise (α~1) is associated with a high complexity and is present in many natural, healthy, unperturbed systems (Duarte & Zatsiorsky, 2001). Deviations from this complexity range might result in pathophysiological disturbances (Duarte & Zatsiorsky, 2001; Hausdorff et al., 1995). Perhaps, the generally greater than 1 scaling exponent α in our study is an expression of the increased postural challenge caused by the stance position with eyes closed. Although the scaling exponent α does not decrease to a value close to or below 1, a reduction could be observed in the mediolateral direction at the cost of an increase in the anteroposterior direction with light touch.

It might be possible that with light contact the dynamics of sway became more direction-specific. Participants stood in Tandem-Romberg stance, which introduces imbalance especially in the mediolateral direction. Therefore, this direction might have become more task-goal relevant in terms of the utilization of the haptic signal for the control of sway. These effects in the mediolateral direction occurred despite the contact point being orientated along the orthogonal, anteroposterior direction. Effects might be even stronger if the contact point is positioned along the mediolateral axis (Jeka *et al.*, 1998). We placed the contact point on the midline to enable quick switching between the two hands as two force-torque sensors were not available to us for placement of one contact point on each side.The sway dynamics do not show a general effect of rPPC disruption. Instead, results show an increase in the scaling exponent α after disruption of the rPPC with fingertip contact of the non-dominant, contralateral hand. It might be that the disruption led to a non-optimal integration of haptic information for body sway control. Ishigaki et al. (2016) demonstrated that processing of a haptic signal when it contains information about body sway relative to an earth-fixed reference reduces cortical activity in the contralateral left-hemisphere parietal lobe as determined by EEG. Unfortunately, they did not assess the effect of contact with the non-dominant (left) hand. We would expect similar contralateral activity reductions in the right-hemisphere parietal lobe.

We did not find an increase of the scaling exponent α in the dominant hand after lPPC disruption. It might simply be that we missed the adequate target location in the left-hemisphere parietal lobe to induce any disruptive effects. It might also be possible, however, that differences between the hemispheres exist with respect to the processing of tactile feedback for sway control. In a previous study, we did not find any disruptive effects of rTMS over the left IPG and left middle frontal gyrus on steady-state body sway with LT (Johannsen *et al.*, 2015). It may be that a disruption of the left-hemisphere was compensated by other brain regions for example the rPPC.

Figure 6 summarizes a simple functional model of interhemispheric interaction, which could underlie our effect patterns. Assuming that rPPC is part of a neural architecture which controls active exploration of the postural stability state opposed by other structures which regulate postural stiffness, rPPC might utilize the haptic signal at the fingertips for this task. rPPC may be disposed to processes haptic information in ego-centric reference frames (Longo *et al.*, 2010; Medina & Coslett, 2010) from both hands, while lPPC processesand relays haptic information from the contralateral hand only (Fig. 6a). If rPPC is disrupted by cTBS, active stability state exploration may be impaired leading to reduced body sway (Fig. 6b). In addition, the utilization of haptic information for sway control from both hands may be affected. In terms of the sway dynamics, a deficit becomes apparent for the contralateral (relative to rPPC), non-dominant hand as the left hemisphere can still process and relay in a signal from the contralateral (relative to lPPC), dominant hand. Finally, if lPPC is disrupted by cTBS (Fig. 6c), only processing of the dominant hand's haptic information is impaired, which can be compensated by rPPC's own access to ipsilateral haptic information. For example, Borchers *et al.* (2011) reported a stroke patient, who demonstrated a proprioceptive deficit for both hands after a right postcentral lesion. Ishigaki et al. (2016), however, did not report bilateral activity changes during quiet stance with light touch but exclusively in the dominant hemisphere contralateral to the contacting hand. As both hemispheres were undisturbed physiologically in their experiment, it may be that any ipsilateral activity changes in the right hemisphere were suppressed.

Continuous TBS over the right or left PPC had no effect on the applied finger force and its variability. Even though average contacting force exceeded 1N, we still consider it a light touch since the applied forces were still not sufficient to provide mechanical support. Moreover, we argue that the light touch in our experiment is a more natural evolving light touch as we tried to avoid turning it into an explicit precision task by including online force feedback. It might be possible, however, that the applied touch in our experiment is processed differently than light touch of lesser than 1N. Jeka and Lackner (1994) reported that feedback delays between fingertip forces and postural adjustments were much longer and the coupling weaker -with contact below 1 N compared to contact with unconstrained forces showing shorter time lags and stronger coupling between fingertip forces and postural adjustments. In this respect the latter might resemble classical supraspinal, long-latency reflexes. Average contact forces in the unconstrained condition in Jeka and Lackner (1994b), however, exceeded 4 N, which is at least twice the amount of contact forces in our present study. Whether the processing of haptic feedback below 1 N or above 4 N is linked with a continuous functional gradient or whether a discontinuity exists between these two ranges is unknown to date and worth further investigation. As contact forces in our present study are closer to the 1 N range, we suggest that the haptic signals in our study should still be considered ‘light’ but we cannot exclude the possibility that this was the reason disruption of the PPC led to no changes in the level of sway specifically with light touch.

In conclusion, we replicated the traditional effect of light touch on body with decreased sway variability but showed direction-specific changes in its complexity. Moreover, we showed that overall sway variability decreases, in addition to the light touch effect, while the sway complexity increases when utilizing haptic information from the non-dominant, contralateral hand after rPPC disruption. We speculate that an increase in postural stiffness could result from lowered inhibition of stiffness regulation by a disrupted process, which is engaged in actively exploring the body’s stability state. We propose a simple functional model of interhemispheric interactions, which could explain our results pattern by the assumption of an asymmetry between the rPPC and lPPC regarding bilateral utilization of haptic information for the control of body sway.

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Abbreviations:

AP: Anteroposterior

CoP: Center-of-Pressure

DFA: Detrended Fluctuation Analysis

IPG: Inferior Parietal Gyrus

ML: Mediolateral

TBS: Theta Burst Stimulation

TMS: Transcranial Magnetic Stimulation

PPC: Posterior Parietal Cortex

SD: Standard Deviation

Competing interests

The authors declare no conflict of interest.

Author contributions

DK and LJ contributed equally to the study design, data collection, data analysis and manuscript preparation. JH contributed to study design and manuscript preparation.

Data accessibility

The experimental data will be accessible via the institutional media repository of the Technical University Munich (https://mediatum.ub.tum.de).

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Figure legends

Figure 1. (A) An illustration of real-time neuronavigation for a participant. Black circles mark the stimulation location in the left and right PPC. (B) A sample trial for single participant. Normal contact force and mediolateral CoP rate of change are plotted across the time course of 140 s trial. (C) Generic overview of the two stimulation sessions.

Figure 2. The time course of mediolateral sway across 20 bins of 500 ms width at contact onset and removal. The black lines indicate body sway variability before cTBS and the dashed lines following cTBS. Error bars indicate standard error of the mean. PPC: posterior parietal cortex.

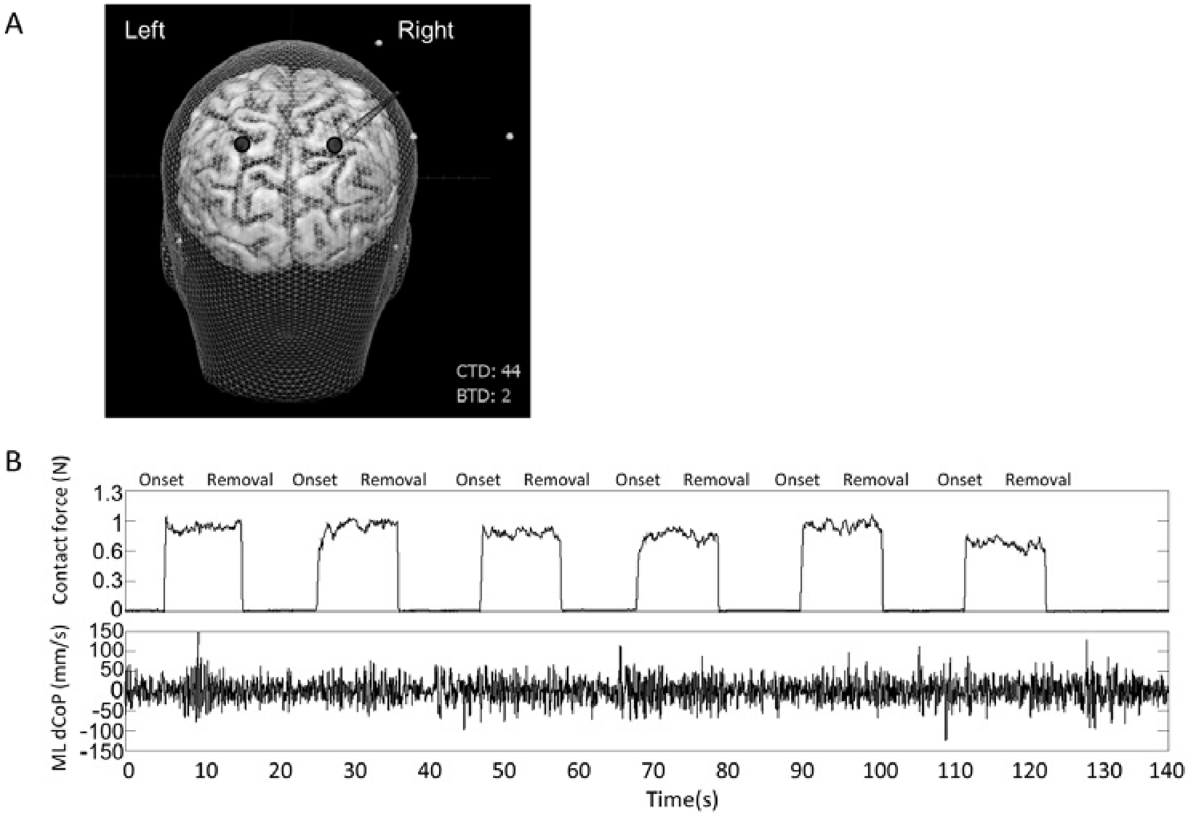
Figure 3. Grand averaged body sway variability as a function of stimulation location before (light grey points) and after (dark grey points) cTBS for the mediolateral (A) and anteroposterior direction (B). Horizontal bars indicating the mean value averaged across all participants. *: $p<0.05$. +: $p<.10$. lPPC: left posterior parietal cortex. rPPC: right posterior parietal cortex.

Figure 4. Scaling exponent as a function of light touch contact for the mediolateral and anteroposterior direction. Horizontal bars indicating the mean value averaged across all participants. *: $p<0.05$.

Figure 5. Scaling exponent as a function of touch contact with the dominant and non-dominant hand before (black points) and after (light grey points) cTBS for (A) Left PPC stimulation, (B) Right PPC stimulation and (C) Sham stimulation. Horizontal

bars indicating the mean value averaged across all participants. *: $p<0.05$. lPPC: left posterior parietal cortex. rPPC: right posterior parietal cortex.

Figure 6. A simplistic functional model of interhemispheric interactions for active stability state exploration. (A) No cTBS disruption. (B) cTBS over the right parietal cortex. (C) cTBS over the left parietal cortex. lPPC: left posterior parietal cortex. rPPC: right posterior parietal cortex. Lightning symbol: cTBS disruption. X: dysfunction.



C

Session 1

- Pre-cTBS (12 min.)
- Threshold estimation (15 min.)
- cTBS stimulation (60 sec.)
- Post-cTBS (12 min.)

Session 2

- Pre-Sham (12 min.)
- Sham stimulation (60 sec.)
- Post-Sham/Pre-cTBS (20 min.)
- cTBS stimulation (60 sec.)
- Post-cTBS (12 min.)

Figure 1.

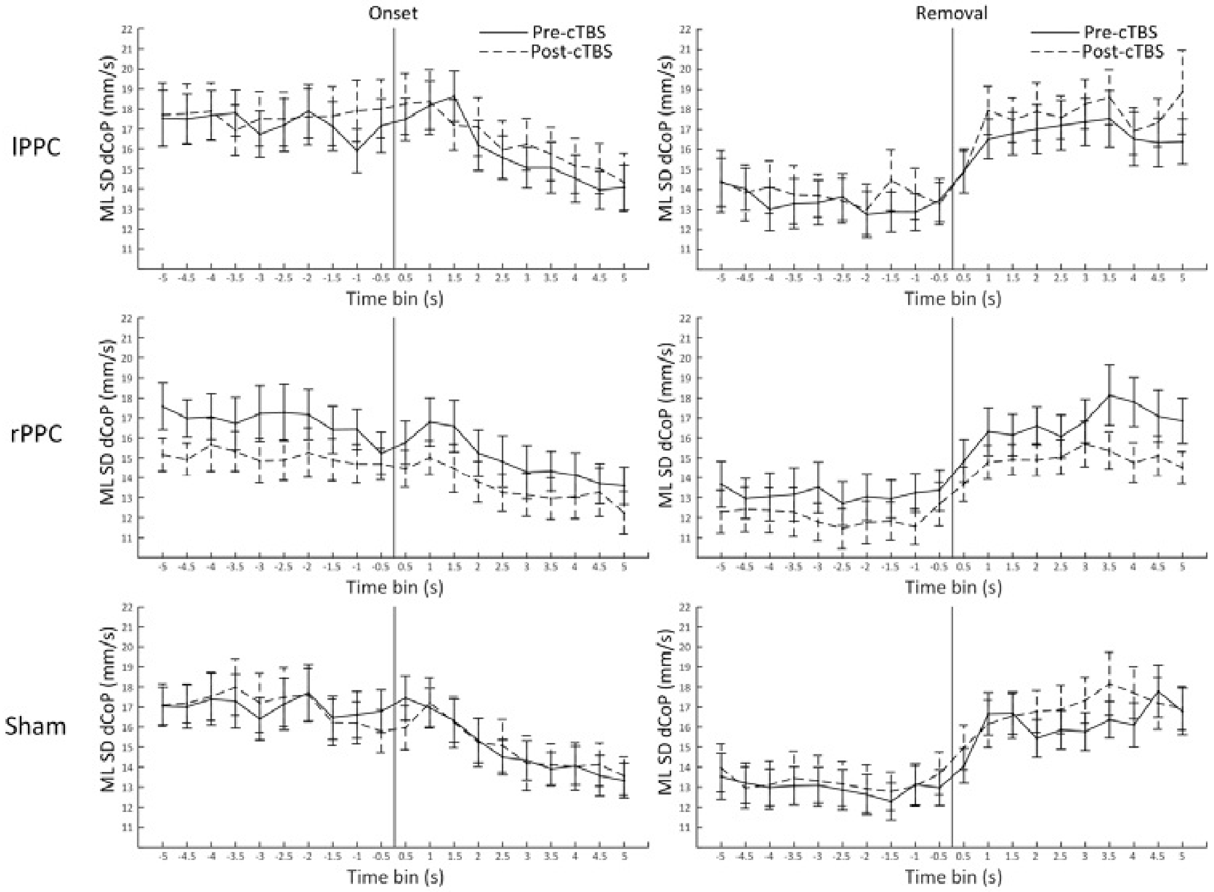
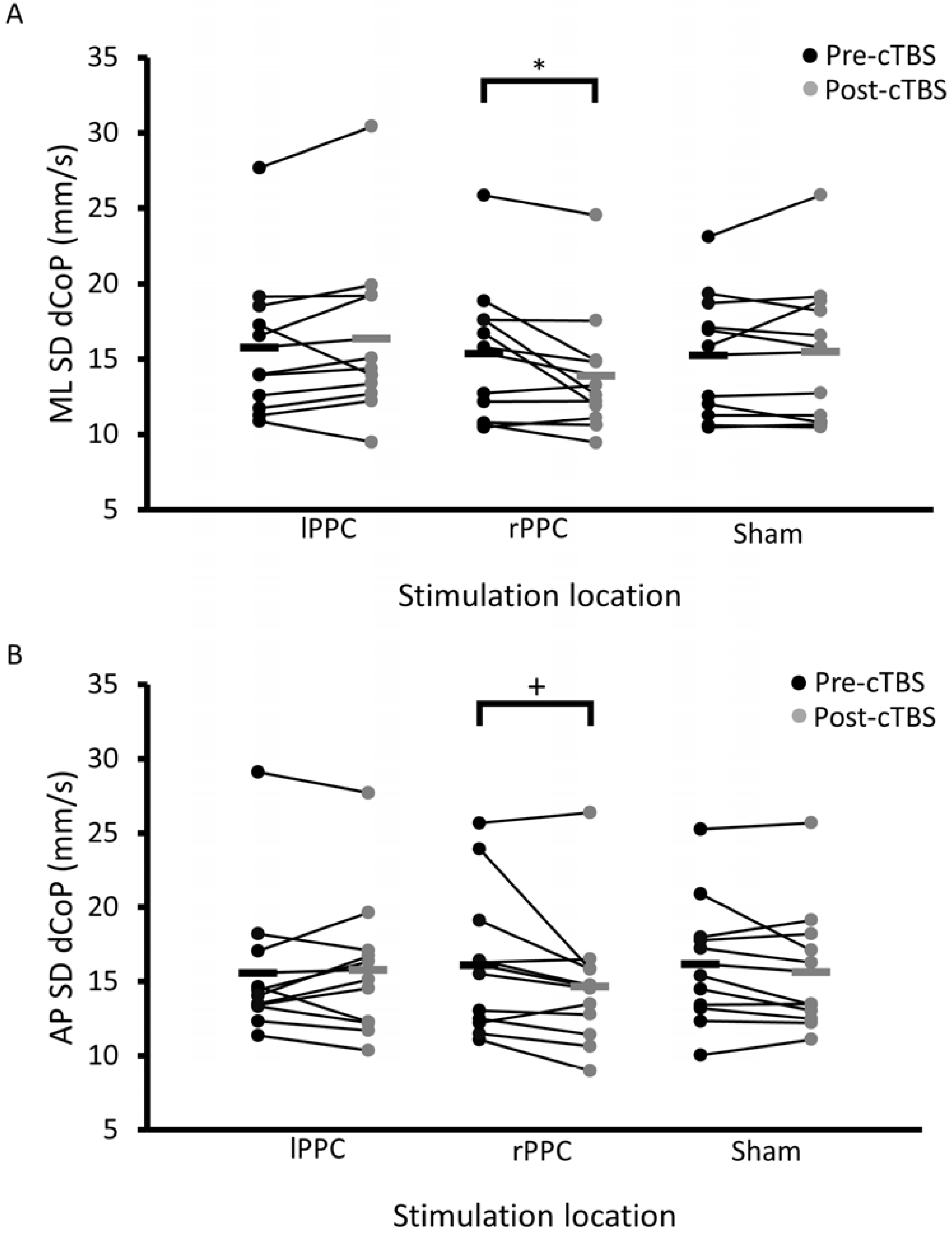

Onset
Removal
Pre-cTBS
Post-cTBS
lPPC
rPPC
Sham
ML SD dCoP (mm/s)
22
21
20
19
18
17
16
15
14
13
12
11
-5
-4.5
-4
-3.5
-3
-2.5
-2
-1.5
-1
-0.5
0.5
1
1.5
2
2.5
3
3.5
4
4.5
5
Time bin (s)

Figure 2.


A
ML SD dCoP (mm/s)
35
30
25
20
15
10
5
*
● Pre-cTBS
● Post-cTBS
lPPC
rPPC
Sham
Stimulation location
B
AP SD dCoP (mm/s)
35
30
25
20
15
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+
● Pre-cTBS
● Post-cTBS
lPPC
rPPC
Sham
Stimulation location

Figure 3.

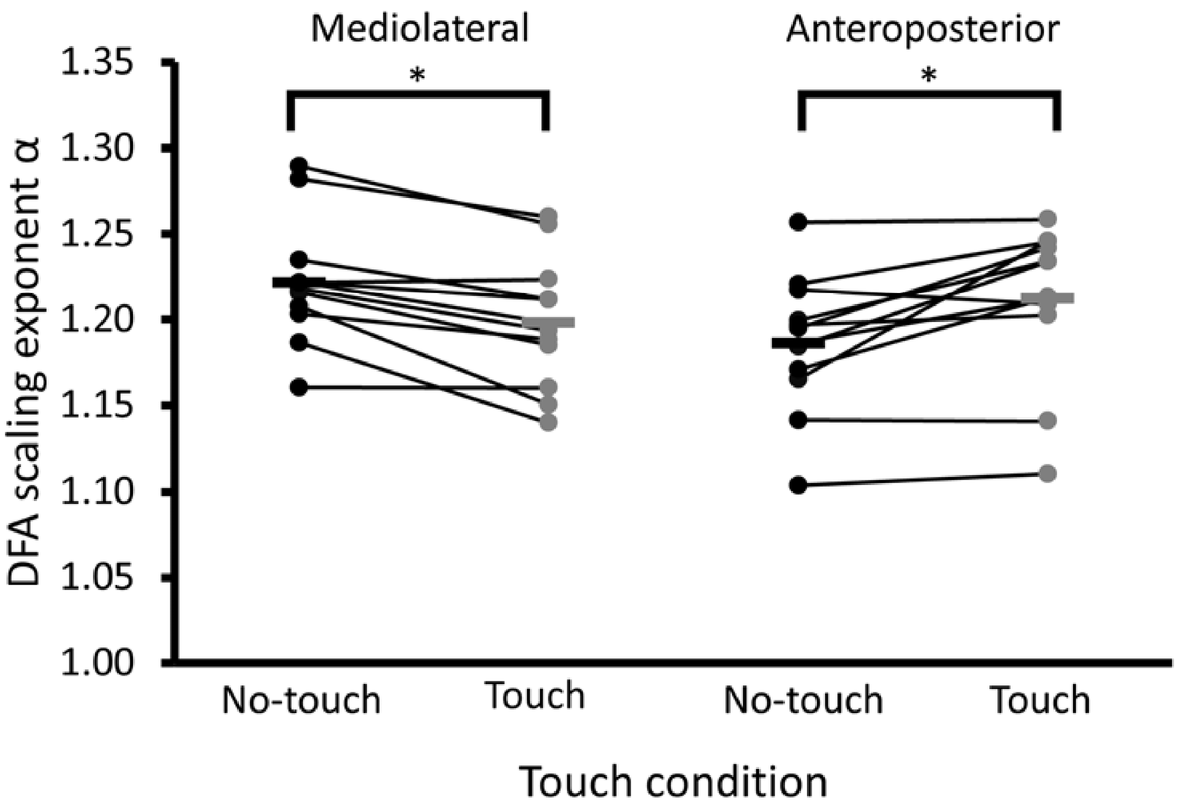
Mediolateral
Anteroposterior
*
*
1.35
1.30
1.25
1.20
1.15
1.10
1.05
1.00
DFA scaling exponent α
No-touch
Touch
No-touch
Touch
Touch condition

Figure 4.

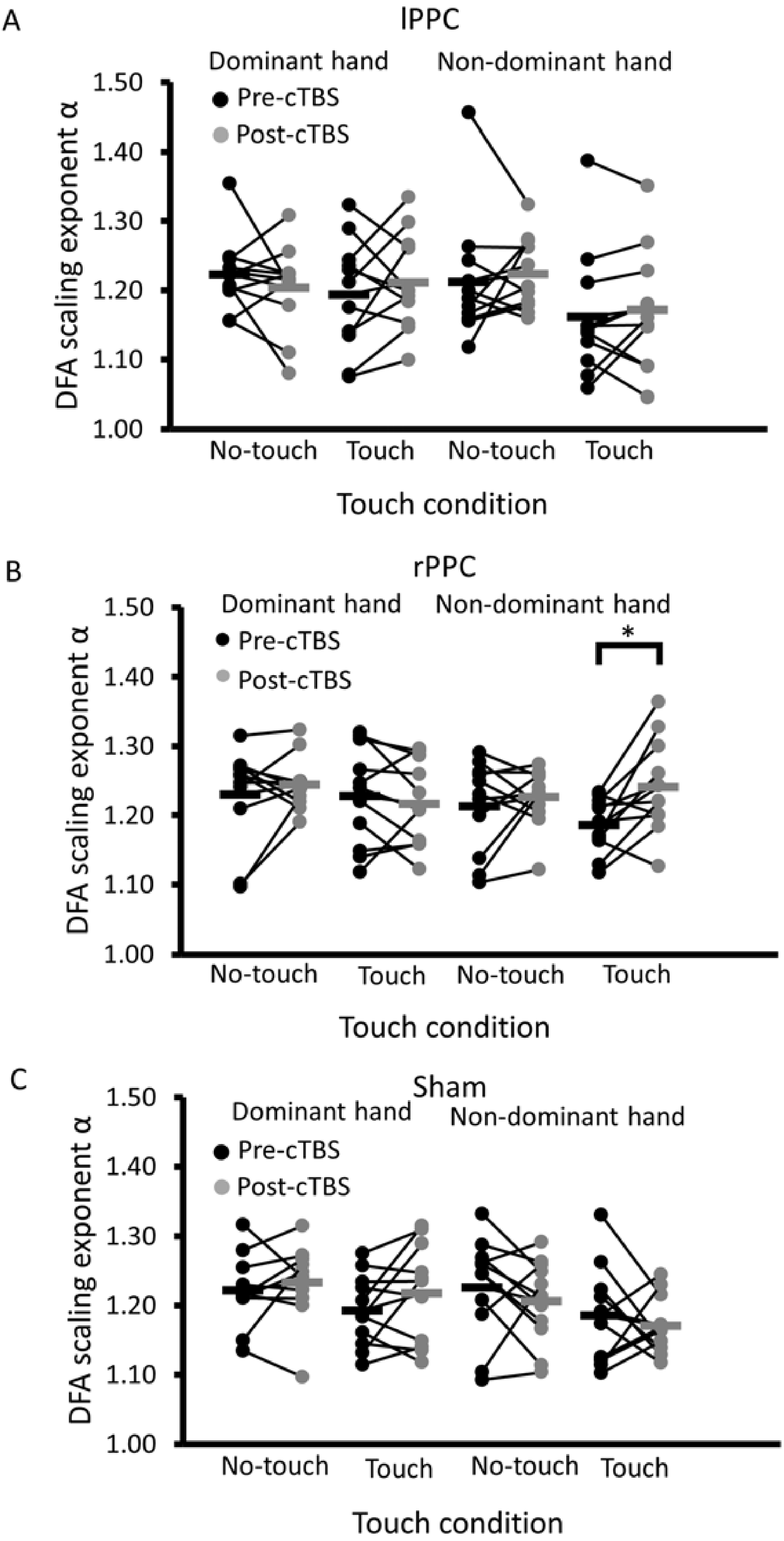
A
lPPC
Dominant hand
Non-dominant hand
● Pre-cTBS
● Post-cTBS
DFA scaling exponent α
1.50
1.40
1.30
1.20
1.10
1.00
No-touch
Touch
No-touch
Touch
Touch condition
B
rPPC
Dominant hand
Non-dominant hand
● Pre-cTBS
● Post-cTBS
*
DFA scaling exponent α
1.50
1.40
1.30
1.20
1.10
1.00
No-touch
Touch
No-touch
Touch
Touch condition
C
Sham
Dominant hand
Non-dominant hand
● Pre-cTBS
● Post-cTBS
DFA scaling exponent α
1.50
1.40
1.30
1.20
1.10
1.00
No-touch
Touch
No-touch
Touch
Touch condition

Figure 5.

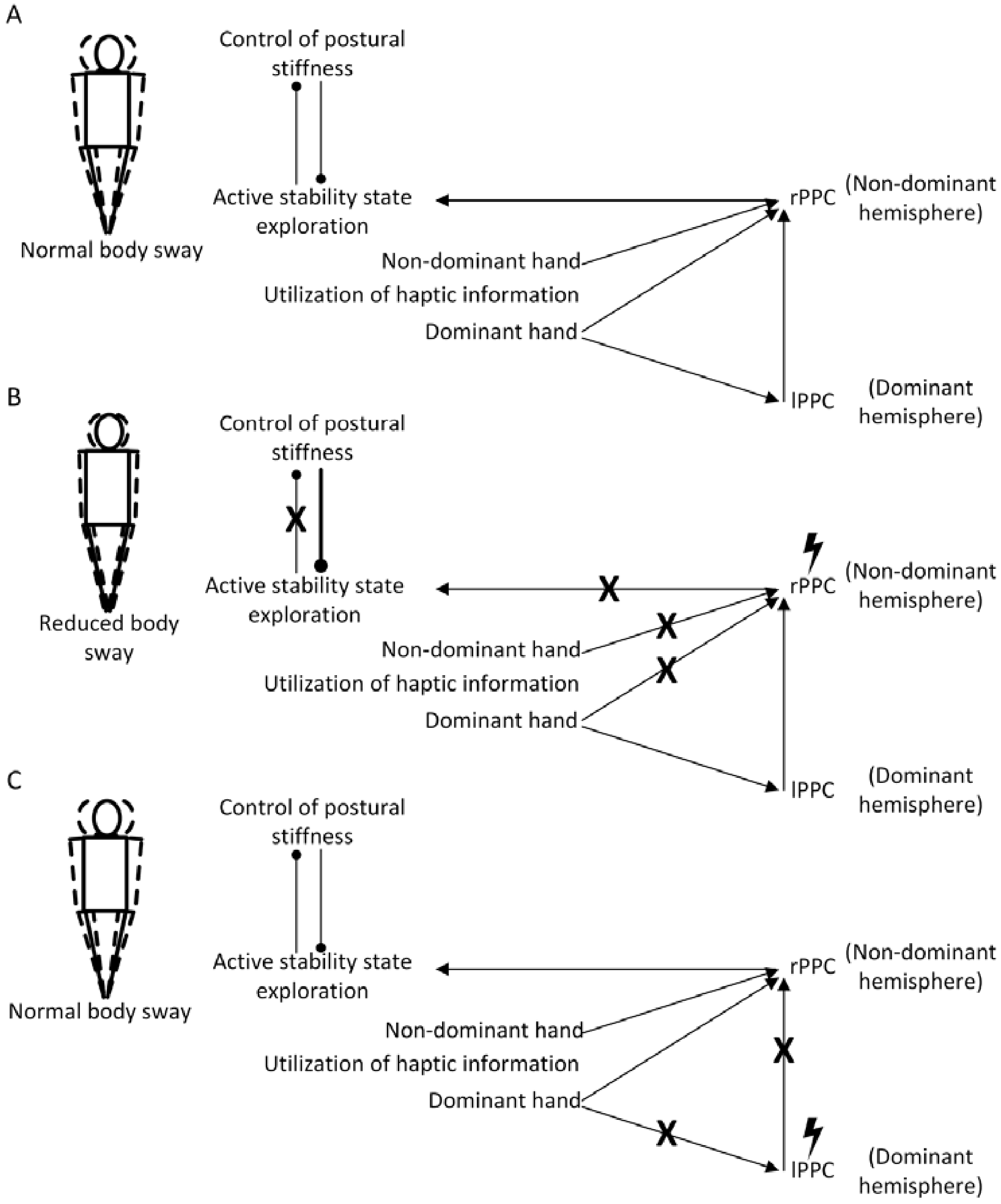
A
Control of postural stiffness
Active stability state exploration
Normal body sway
Non-dominant hand
Utilization of haptic information
Dominant hand
rPPC
(Non-dominant hemisphere)
lPPC
(Dominant hemisphere)
B
Control of postural stiffness
Active stability state exploration
Reduced body sway
Non-dominant hand
Utilization of haptic information
Dominant hand
rPPC
(Non-dominant hemisphere)
lPPC
(Dominant hemisphere)
C
Control of postural stiffness
Active stability state exploration
Normal body sway
Non-dominant hand
Utilization of haptic information
Dominant hand
rPPC
(Non-dominant hemisphere)
lPPC
(Dominant hemisphere)

Figure 6.

3.4 Summary of study IV

Following the results of the previous study, suggesting that disruption of the rPPC leads to increased stiffness, it was necessary to assess how increased postural stiffness influences the ability to react to unforeseen perturbations. It was hypothesized that the benefit of light touch would be amplified in the more dynamic context of an external perturbation, reducing body sway and muscle activations before, at and after a perturbation. Furthermore, it was expected that sway stabilization would be impaired following disruption of the right Posterior Parietal Cortex as a result of increased postural stiffness. As in the previous study, the experiment was divided into three sessions, one to acquire a brain scan for real-time neuronavigation and two experimental sessions. Again, each experimental session consisted of a balance pre-test, the application of TMS and a balance post-test. Thirteen young adults stood blindfolded in Tandem-Romberg stance on a force plate and were required either to keep light fingertip contact to an earth-fixed reference point or to stand without fingertip contact. In order to perturb participants, they were pushed in medio-lateral direction by a robotic arm with either 1%, 4% or 7% of their respective body weight. Each balance test consisted of 4 blocks before TMS stimulation and 8 blocks after, alternating between light touch and no touch conditions. TMS consisted of continuous Theta Burst Stimulation (cTBS) of an intensity of 80% of the passive motor threshold for 60 seconds or a sham stimulation over the right Posterior Parietal Cortex. Results revealed a strong light touch effect with light touch decreasing the immediate sway response, steady state sway following re-stabilization, as well as muscle activity of the Tibialis Anterior and Gastrocnemius. Furthermore, there was a gradual decrease of muscle activity over time, which indicates an adaptive process following exposure to repetitive trials of perturbations. Contrary to the previous study and the hypothesis, cTBS over the rPPC did not lead to increased postural stiffness. However, there was an unexpected effect of cTBS stimulation in terms of improvements of the adaptive process. After disruption of the rPPC muscle activity of the Tibialis Anterior was decreased even greater, compared to sham, with a trend for the same effect for the Gastrocnemius. It might be possible that rPPC disruption enhanced the intra-session adaptation to the disturbing effects of the perturbation.

Contributions:

The experiment was conceptualized by David Kaulmann, with feedback provided by Leif Johannsen Participant acquisition, data collection and TMS application was carried out by

David Kaulmann. The robotic arm was operated by Matteo Saveriano, supporting the data collection as well. Data and statistical analysis was also performed by David Kaulmann using Matlab and R, with Matteo Saveriano providing processed data of the robotic arm. The manuscript for the publication was written by David Kaulmann, with Leif Johannsen and Joachim Hermsdörfer providing feedback and corrections.

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PLOS ONE

RESEARCH ARTICLE

Stabilization of body balance with Light Touch following a mechanical perturbation: Adaption of sway and disruption of right posterior parietal cortex by cTBS

David Kaulmann[1] *, **Matteo Saveriano**[2], **Dongheui Lee**[3,4], **Joachim Hermsdörfer**[1],
Leif Johannsen[5]

1 Department of Sport and Health Sciences, Human Movement Science, Technische Universität München, Munchen, Germany, **2** Department of Computer Science, Intelligent and Interactive Systems, University of Innsbruck, Innsbruck, Austria, **3** Human-centered Assistive Robotics, Electro- and Information Technology, Technische Universität München, Munchen, Germany, **4** Institute of Robotics and Mechatronics, German Aerospace Centre, Cologne, Germany, **5** Institute of Psychology, Cognitive and Experimental Psychology, RWTH Aachen, Aachen, Germany

* david.kaulmann@tum.de

Abstract

Light touch with an earth-fixed reference point improves balance during quite standing. In our current study, we implemented a paradigm to assess the effects of disrupting the right posterior parietal cortex on dynamic stabilization of body sway with and without Light Touch after a graded, unpredictable mechanical perturbation. We hypothesized that the benefit of Light Touch would be amplified in the more dynamic context of an external perturbation, reducing body sway and muscle activations before, at and after a perturbation. Furthermore, we expected sway stabilization would be impaired following disruption of the right Posterior Parietal Cortex as a result of increased postural stiffness. Thirteen young adults stood blindfolded in Tandem-Romberg stance on a force plate and were required either to keep light fingertip contact to an earth-fixed reference point or to stand without fingertip contact. During every trial, a robotic arm pushed a participant's right shoulder in medio-lateral direction. The testing consisted of 4 blocks before TMS stimulation and 8 blocks after, which alternated between Light Touch and No Touch conditions. In summary, we found a strong effect of Light Touch, which resulted in improved stability following a perturbation. Light Touch decreased the immediate sway response, steady state sway following re-stabilization, as well as muscle activity of the Tibialis Anterior. Furthermore, we saw gradual decrease of muscle activity over time, which indicates an adaptive process following exposure to repetitive trials of perturbations. We were not able to confirm our hypothesis that disruption of the rPPC leads to increased postural stiffness. However, after disruption of the rPPC, muscle activity of the Tibialis Anterior is decreased more compared to sham. We conclude that rPPC disruption enhanced the intra-session adaptation to the disturbing effects of the perturbation.

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Abbreviations: CNS, Central Neuro System; CoG, Centre of Gravity; CoM, Centre of Mass; CoP, Centre of Pressure; cTBS, continuous Theta Burst Stimulation; dCoP, differentiated Centre of Pressure; IPG, Inferior Parietal Gyrus; LT, Light Touch; PPC, Posterior Parietal Cortex; rTMS, repetitive Transcranial Magnetic Stimulation; rPPC, right Posterior Parietal Cortex; TMS, Transcranial Magnetic Stimulation.

Introduction

The main objective for the control of body posture and balance is to stabilize upright standing against the pull of gravity or any other external forces and to prevent the body from toppling over. This is achieved by keeping the Centre of Mass' (COM) vertical projection onto the ground (Centre of Gravity, CoG) within the support boundaries. In order to maintain balance, the Central Nervous System (CNS) relies on sensory feedback processed by the visual, vestibular and somatosensory systems [1]. However, in addition to its primary senses the CNS is also able to use information from secondary afferent channels, such as the skin, as long sway-related information is conveyed. Light touch (LT) with an earth-fixed reference point has been shown to decrease sway variability and improve balance during quite stance [2] but also in dynamic situations, such as when compensating an either foreseeable or unpredictable external perturbation. For example, Dickstein and colleagues [3] demonstrated that Light Touch facilitates the scaling of postural compensation in response to horizontal support surface translations. Furthermore, Light Touch results in faster stabilization and reduced body sway following both externally and self-imposed body balance perturbations [4]. Imposing the sudden release of a backward load to the trunk, Martinelli et al. [5] reported that Light Touch reduced and slowed Centre-of-Pressure (CoP) displacement as well as decreased activity in the lower limbs' Gastrocnemius muscles under challenging sensory conditions. Johannsen and co-workers [6] also provided evidence for the benefit of Light Touch in dynamic postural contexts by exerting abrupt backward perturbations onto participants standing on a compliant springboard under different conditions of visual feedback. The utilization of Light Touch stabilized balance and decreased thigh muscle activity by up to 30%, which indicates that Light Touch optimizes mechanical and metabolic costs of balance compensation following a perturbation to a compliant support surface [6].

Although responses to postural perturbations are faster than voluntary movements, the observation that long-latency reflexes are sensitive to the postural context suggests involvement of supraspinal neural circuits including the cerebral cortex [7]. Several studies implied a role of cortical neural circuits in the control of posture when anticipating a perturbation to body balance. Cortical potentials preceding self-initiated perturbations, as well as predictable external perturbations show differences in amplitude as well as temporal characteristics [8], which might represent adjustments in a central set prior to the onset of a known perturbation. Depending on alterations in the cognitive state, such as changes in the cognitive load or attentional focus, initial sensory-motor conditions, prior experience and prior warning of a perturbation influences the central set enabling adaptations of the postural response to a perturbation [7]. Several cortical areas have been identified for playing a role in the control of balance, mainly the primary motor cortex, the somatosensory cortex and the posterior parietal cortex (PPC). For example, the primary motor cortex is responsible in the regulation of induced postural responses of the lower limbs [9]. Taube et al. [9] applied a single pulse TMS paradigm to demonstrate that corticospinal projection to the soleus muscle facilitates long-latency responses following abrupt backward translations of the support. Similarly, the sensorimotor cortex has been reported to play a role not only in the integration and in processing of sensory information, but also in adjusting the central set to modify externally triggered postural responses [7]. In addition, involvement of the supplementary motor area in motor planning and preparation for an adequate response to perturbations has been reported [10–12]. Contrasting balance perturbations caused by horizontal translations of a support surface with and without an auditory pre-warning, Mihara et al. [10] used functional near-infrared spectroscopy to demonstrate that both the left-hemisphere supplementary motor area and the right-hemisphere posterior parietal cortex increased activation, when preparation for the upcoming perturbation was possible. This observation argues for an involvement of both areas in the anticipation and probably also compensation of an expected postural imbalance. Likewise, An et al. [13] who investigated the contribution of the sensory motor cortex and the PPC to recovery responses following unpredictable perturbations during standing or walking. Both areas showed a suppressed activity in the alpha band during periods of balance recovery [13]. The significant role of the posterior parietal cortex in the stabilization of balance is further corroborated by Lin et al. [14]. They showed that a lesion in the posterior parietal cortex following stroke leads to reactive postural control deficit, such as impaired recruitment of paretic leg muscles and a more frequent occurrence of compensatory muscle activation patterns compared to controls. Lin et al. [14] concluded that the PPC is part of a neural circuitry involved in reactive postural control in response to lateral perturbations.

Regions of the cerebral cortex are also involved in the processing and integration of the sensory information from the fingertips when utilizing Light Touch for postural control. Ishigaki et al. [15] demonstrated involvement of the left primary sensorimotor cortex and the left posterior parietal cortex in stance control with light tactile feedback. Johannsen et al. [16] investigated how rTMS over the left inferior parietal gyrus (IPG) influences sensory re-organization for the control of postural sway with light fingertip contact. They reported that rTMS over the left IPG reduced overshoot of sway after contact removal, which indicates that this brain region may play a role in inter-sensory conflict resolution and adjustment of a central postural set for sway control with contralateral fingertip contact.

Assuming that an ego-centric reference frame would be the basis of interpreting and disambiguating fingertip Light Touch for sway control in a quiet upright stance with transitions between postural states with and without Light Touch feedback, we investigated the effects of disrupting the left- and right hemisphere PPC using continuous Theta Burst Stimulation (cTBS) [17]. We expected that disruption of the right Posterior Parietal Cortex would impair integration of Light Touch into the postural control loop and attenuate the effect of Light Touch on body sway. These expectations were not confirmed but we demonstrated that rPPC disruption influenced the complexity of body sway with Light Touch of the non-dominant, contralateral hand [17]. In addition, disruption of the rPPC resulted in an overall sway reduction and altered complexity irrespective of the presence of Light Touch. A possible reason could be that rPPC disruption increased overall body stiffness due to lower limb muscular co-contractions and thus reduced body sway [18]. Sway reduction does not mean, however, that participants are intrinsically more stable. Variability is a means of the postural control system to achieve a specific task goal while at the same time being more able to react flexibly to possible external balance perturbations [19]. Thus, it can be argued that the reduction in sway reflects an unfavourable effect in terms of participants becoming less adaptive and less able to compensate unexpected perturbations [20] after rPPC disruption.

Taking into account the well documented light-touch-related facilitation of balance stabilization, following an external perturbation [3,4,5,6] we implemented a perturbation paradigm to assess the influence of rPPC disruption on dynamic stabilization of body sway with and without Light Touch. In previous studies, however, perturbations consisted either of a single constant force or of variable forces but in a blocked design, making perturbations much more predictable, enabling adjustment to a central postural set. In our current study, we intended to make it much more difficult for the participants to predict the force of an upcoming perturbation. Therefore, we randomized three forces on a trial-by-trial basis within a block of either Light Touch or no touch. We hypothesized that the benefit of Light Touch would be amplified in the more dynamic context of an external perturbation to balance, improving the compensation response. We also expected that the immediate response to a perturbation and sway stabilization in terms of its time constant would be affected expressing an increase in postural stiffness following rPPC disruption.

Methods

Participants

Thirteen healthy right-handed young adults (age = 26 ± 2 (SD); 10 women and 3 men) were recruited for this study, using the faculties own blackboard. Inclusion criteria were (1) no neurological or musculoskeletal disorders, (2) no balance impairment and (3) no known history of epilepsy or reported seizures. All participants were informed about the study protocol and signed a written informed consent. The study was approved by the Clinical Research Ethics committee of the Medical School of the Technical University Munich.

Study protocol, apparatus and experimental procedure

The study protocol comprised of two single TMS sessions in the balance lab. The order of stimulation locations (rPPC or sham TMS) was randomized across participants. Stimulation sessions were separated by at least 24 hours. Each experimental testing session consisted of three parts: a balance pre-test, 60 seconds of cTBS and a balance post-test. During the pre- and post-test participants stood in Tandem-Romberg stance on a force plate (600Hz; Bertec FP4060-10, Columbus, Ohio, USA), with their eyes blindfolded and instructed to stand quietly but relaxed and not to attempt to minimize body sway.

Participants were required either to keep light haptic fingertip contact with their dominant hand to an earth-fixed reference point or to stand without fingertip contact. Participants practiced keeping Light Touch with the reference point prior to the start of the experiment receiving verbal feedback about the strength of the contact force until they felt comfortable maintaining Light Touch below 1 N. During the experiment, however, participants did not receive feedback about contact force to prevent contacting from becoming an explicit, attention-demanding precision task. The earth-fixed contact reference point was placed in front of the participants. They held one arm slightly angled in front of the body and reaching straight forward. The other arm remained passive at the side of their body (Fig 1).

Body kinematics (4 Oqus 500 infrared cameras; 120 Hz; Qualisys, Göteborg, Sweden) and forces and torques at the fingertip reference contact location (6DoF Nano 17 force-torque transducer; 200 Hz; ATI Industrial Automation, Apex, USA) were also acquired. To capture body motion, reflective markers were placed at the contacting fingertip, wrist, elbows, shoulders, C7, Sternum, hip, knees and ankles. Additionally, surface EMG (1kHz) of the Gastrocnemius, Soleus and Tibialis Anterior of the posterior supporting leg was recorded to measure muscle activity (Trigno Wireless PM-W05, Delsys, Natic, MA, USA).

During every single standing trial, a robotic arm (KUKA LBR4+, Augsburg, Germany) exerted a push to participants at their right shoulder in medio-lateral direction. In order to make the next perturbation force as unpredictable as possible, the force of a lateral push was exerted with either 1%, 4% or 7% of their respective body weight in a randomized order in a block consisting of 6 trials (2 trials for each push force). Using a percentage of the body weight for every single participant, results in different absolute forces for the participants. However, relative force of the push for the perturbation is equalized for across participants. Table 1 shows the absolute peak push forces in N for the conditions averaged over all participants.

A testing session consisted of 4 blocks before the cTBS application (pre-test) and 8 blocks after (post-test). The blocks alternated between Light Touch (LT) and No Touch (NT) conditions. For a comparison between sway before and after the cTBS application, sway was averaged across the NT and LT blocks respectively (pre-test: NT = blocks 1+3, LT = blocks 2+4; post-test: NT = blocks 6+8+10+12; LT = blocks 5+7+9+11). Duration of a single trial was 20 seconds, with the lateral push always applied at 4.5 seconds after the start of a trial (Fig 2).

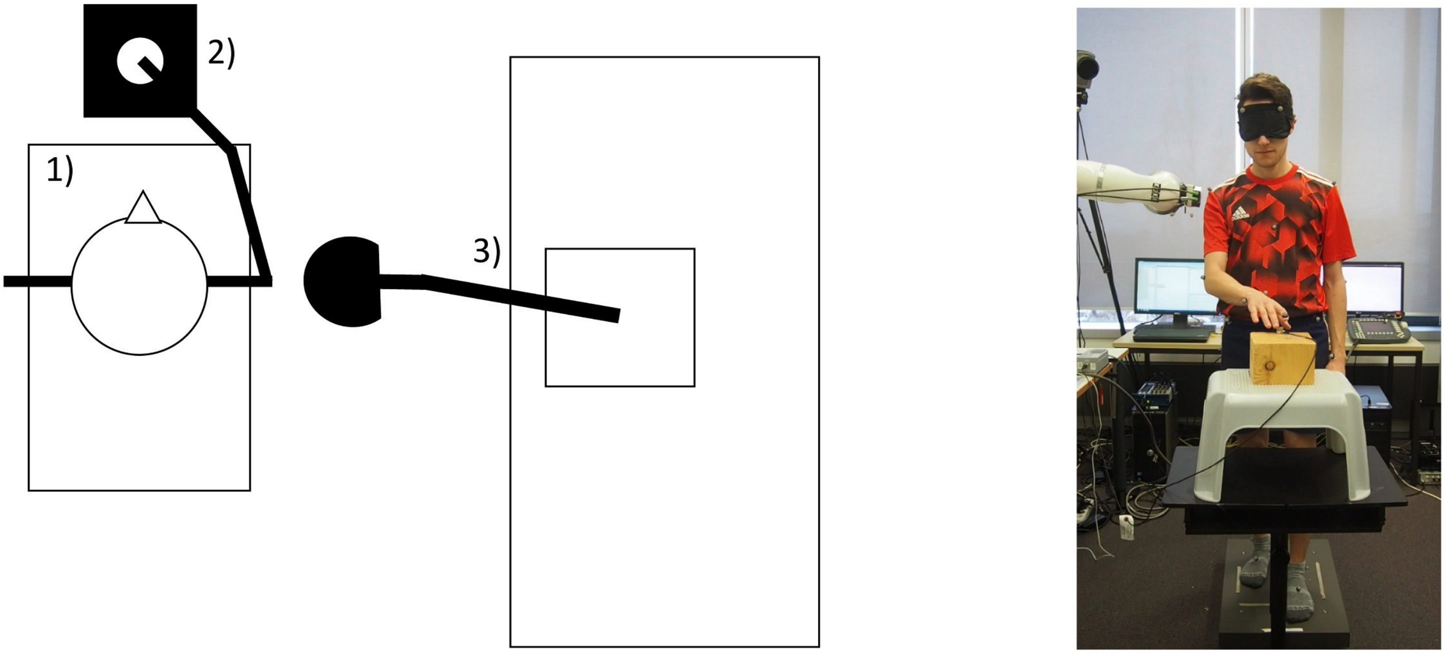

Fig 1. Experimental set up as seen from above. (1) Force plate, (2) contact reference point on a waist high stand and (3) Robotic arm mounted on a table.

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Neuronavigation and TMS protocol

During cTBS stimulation, participants were seated comfortably on a reclined chair facing a wall and keeping their head straight. We applied continuous Theta Burst Stimulation (cTBS) of an intensity of 80% of the passive motor threshold for 60 seconds over the rPPC (PMD70-pCool; MAG & More, Munich, Germany). This protocol is widely used and stimulation effects can last from 20 minutes up to 1 hour (Staines & Bolton [21]. The passive motor threshold was determined by registering the motor evoked potential (MEP) at the musculi interossei dorsales manus of the left hand following a single TMS pulse over the hand representation of the right-hemisphere primary motor cortex. A staircase procedure was used to adjust the pulse intensity until a 50μV MEP could be elicited reliably [22].

Sham stimulation was applied over the same target location as for the cTBS using a sham coil powered at similar intensities, which produced no focussed magnetic induction but created similar acoustics and tactile sensation. (PMD70-pCool-Sham; MAG & More, Munich, Germany).

High-resolution anatomical brain scans were acquired before the study at the University Hospital Großhadern, Center for Sensorimotor Research and consisted of a T1 MPRAGE (3T

Table 1. Push forces averaged over all participants broken down by force push condition and stimulation protocol.

% of Body Weight	Stimulation Protocol	Force (N)
1	Sham	2.99
1	Stim	2.89
4	Sham	6.95
4	Stim	6.01
7	Sham	11.56
7	Stim	10.06

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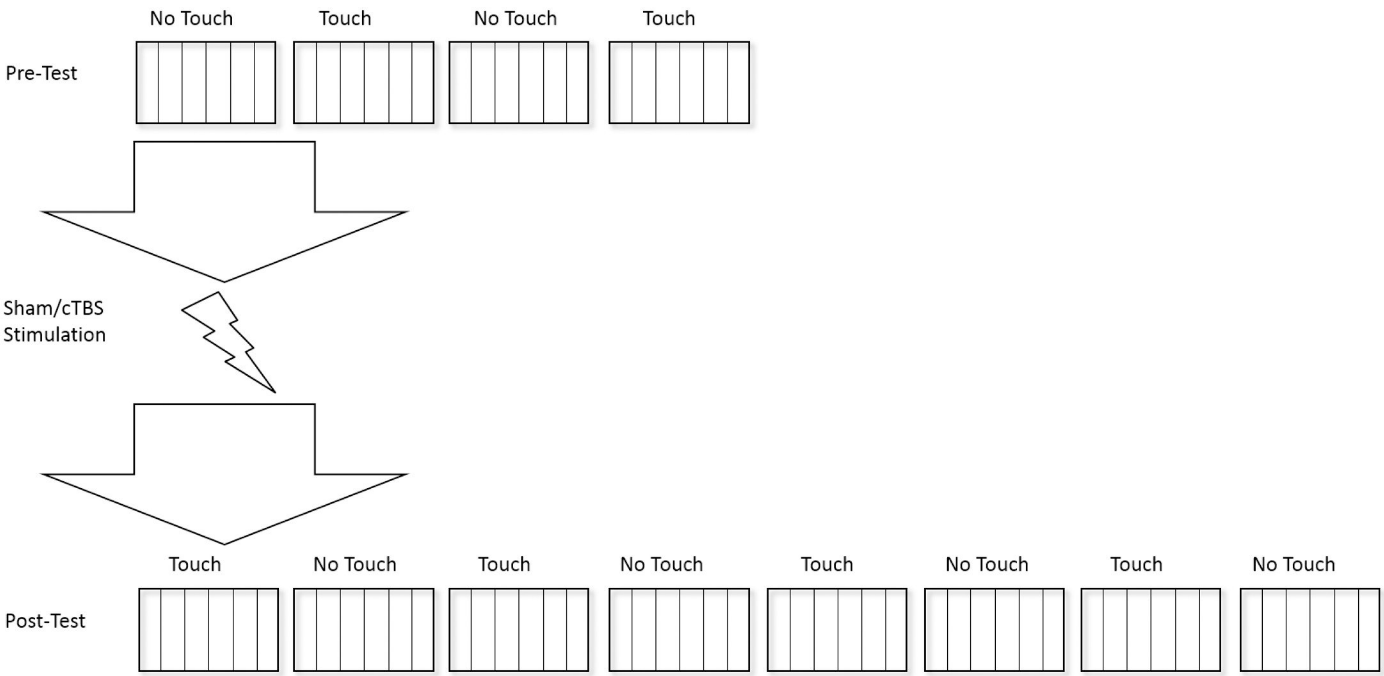

Fig 2. Experimental process. Rectangle boxes represent blocks, separated by lines representing single trials.

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whole-body scanner, Sigma HDx, GE Healthcare, Milwaukee, Wisconsin, USA). In order to define the cTBS target area, we used MNI coordinates (x = 26, y = 258, z = 43) reported in Azañón et al. [23] (2010), who stimulated the right-hemisphere human homologue of macaque ventral intraparietal area. We therefore expected that cTBS would disrupt activity in the Superior Parietal Lobule (SPL; Area 7A) and Intraparietal Sulcus (IPS) of the right hemisphere. Stimulation locations were targeted using real-time neuronavigation software (TMS Neuronavigator, Brain Innovation, Maastricht, Netherlands).

In order to localize the stimulation area for each individual participant, the high-resolution scan was co-registered and normalized to the MNI template.

Data processing and data reduction

All data processing was performed using customized functions scripted in Matlab 2018b (Mathworks, MA, USA). Centre-of-Pressure (CoP) data of the force plate was digitally low-pass filtered with a cut-off frequency of 10 Hz (dual-pass, 4^{th}-order Butterworth). CoP position was differentiated to obtain CoP rate-of-change in m/s(dCoP). In order to characterize balance recovery, we followed a similar approach as applied in Johannsen et al. [4]. The standard deviation of the medio-lateral dCoP (SD dCoP) was calculated for each of 13 temporal bins of 1 s duration before and after the moment of the perturbation. A period of 3 s duration before the perturbation served as an intra-trial sway baseline. Across the 10 post-perturbation bins demonstrating stabilization, we fitted from an exponential decreasing non-linear regression $x(t) = C + A^{*}e^{\left(-\frac{t}{B}\right)}$, from which we obtained the function parameters A (intercept), B (time constant) and C (asymptote). The intercept is derived from the body sway at perturbation (t = 0) and therefore reflects the immediate effect of the perturbation. The time constant represents the rate of stabilization of body sway after the perturbation with shorter time constants indicating faster stabilization. The third parameter, the asymptote, indicates the level of steady-state long-term stabilization.

EMG recordings were band-pass filtered between 10 and 500 Hz, rectified and smoothed by a moving average with 15ms width to obtain the EMG activity envelope of a muscle. For each muscle we extracted peak amplitude, indicating the amount of phasic activity directly following a perturbation and the area-under-the-curve of the activity envelope as an indication of the tonic activity across an entire trial serving as an indication of general muscle activation. EMG activity was then normalized to the first baseline block for NT and LT respectively and percentage of change from baseline was calculated.

Statistical analysis

Data of the robotic device was checked for failures to deliver a forced push with an abrupt impact and immediate withdrawal of the end-effector. Trials in which the robotic arm only continuously shoved participants were excluded. Only successful force pushes were included in the data analysis. Overall there was a success rate of 87%.

Only trials with exponential fits of greater than 75% explained variance were included in the subsequent statistical analysis. In total, 15% of trials did not reach this threshold and were excluded from the statistical analysis. In order to identify possible non-responders to the cTBS stimulation we applied a k-means cluster analysis. K-means cluster analysis is a unsupervised learning algorithm that tries to cluster data based on their similarity, once the amount of desired clusters is defined. We defined 2 clusters (Responder vs. Non-responder) that we wanted data to be grouped into. Data for the intercept, time constant, asymptote, peak amplitude and area under the curve were pooled together and clustered in the two groups of either responders or non-responders. We identified two possible non-responders, leaving us with 11 participants for the statistical analysis. Prior to analysis data was log transformed to fit normal distribution. Parameters were then analysed statistically using a linear mixed model, with four repeated-measures factors (1) hand contact (Touch vs. No Touch), (2) stimulation session (cTBS vs. Sham), (3) Test (pre- vs. post-stimulation) and (4) force push (1% vs 4% vs 7%): (Variable~Stimulation_Session+Hand_Contact+Test+Force_Push+Stimulation_Session*Hand_Contact+Stimulation_Session*Test+Stimulation_Session*Force_Push+Hand_Contact*Test+LT*Force_Push+Test*Force_Push+Stimulation_Session*Hand_Contact*Test+Stimulation_Session*Test*Force_Push+Stimulation_Session*Hand_Contact*Force_Push+Hand_Contact*Test*Force_Push+Stimulation_Session*Hand_Contact*Test*Force_Push + (1 |Subjects)) (Table 2). Fixed effects were "Hand_contact", "Stimulation_Session", "Test" and "Force_Push". Force push was treated as continuous, the others as factors. A post-hoc analysis was carried out to clarify the effects of stimulation session on muscle activity. A linear model with three repeated-measures factors (1) Test (pre- vs. post-stimulation), (2) hand contact (Touch vs. No Touch) and (3) force push (1% vs. 4% vs. 7%) was carried out for both stimulation sessions (sham and cTBS) respectively: (Variable~Test+Hand_Contact+Force_Push+Test*Hand_Contact+Test*Force_Push+Force_Push*Hand_Contact+Test*Hand_contact*Force_push + (1|Subjects)).

We also performed an analysis to investigate progression of sway over time with three repeated-measures factors (1) Block (progression over time), (2) hand contact (Touch vs. No Touch) and (3) stimulation session (cTBS vs. Sham): (Variable~Stimulation_Session+Hand_Contact+Block+Stimulation_Session*Hand_Contact+Stimulation_Session*Block+Stimulation_Session+Hand_Contact*Block+LT+Block+Stimulation_Session*Hand_Contact*Block+Stimulation_Session*Block+Stimulation_Session*Hand_Contact+Hand_Contact*Block+Stimulation_Session*Hand_Contact*Block + (1 |Subjects)) (Table 3). We also

Table 2. Results for Centre of Pressure and EMG.

Measure		P value							
	Light Touch F (1,231)	Test F (1, 231)	Push Force F(2, 231)	Light Touch x Test F(1, 231)	Stimulation protocol x Test F(1, 231)	Test x Push Force F(1, 231)	Light Touch x Push Force F (2, 231)	Light Touch x Stimulation Protocol F(1, 231)	Stimulation protocol x Light Touch x Test F(1, 231)
	Centre of Pressure								
Intercept	< .01	< .001	< .001	< .05	NS	NS	NS	NS	NS
Slope	NS	NS	< .05	NS	NS	NS	NS	NS	NS
Constant	< .001	< .001	< .001	< .001	NS	NS	NS	NS	NS
	Tibialis Anterior								
EMG Integral	< .001	< .001	NS	< .05	< .001	NS	NS	< .05	NS
Peak Amplitude	< .001	< .01	< .01	NS	NS	NS	NS	NS	NS
	Gastrocnemius								
EMG Integral	NS	< .01	NS	NS	NS	NS	NS	NS	NS
Peak Amplitude	< .001	< .001	NS	NS	< .05	NS	NS	< .05	NS
	Soleus								
EMG Integral	NS	NS	NS	NS	NS	NS	NS	NS	NS
Peak Amplitude	< .05	NS	< .001	NS	NS	NS	NS	NS	NS

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performed a post-hoc analysis with specific focus on the first four blocks before the stimulation (Variable ~ Stimulation_Session + Hand_Contact + Block + Stimulation_Session*Hand_Contact + Stimulation_Session*Block + Hand_Contact*Block + Stimulation_Session*Hand_Contact* Block + (1 | Subjects)), investigating whether stimulation protocol had an influence in the pre-test already. This would hint at a session effect rather a stimulation effect.

For statistical significance, a p-value of 0.05 was used. Statistical analysis was carried out using the lme4 package in R-statistics (R version 3.4.0). Model estimates of the two main linear mixed models can be found in the supporting information.

Results

General sway analysis

Fig 3 shows illustrative data of one participant, averaged over all conditions. After the perturbation, the C7 body marker is deflected laterally accompanied by an excursion of the differentiated CoP signal. EMG activity of the Gastrocnemius rises to produce the required torque to compensate the perturbation. As a result, the CoP is accelerated into the opposite direction and C7 returns to the baseline position. EMG activity and CoP settle at pre-perturbation levels again until the end of the trial.

CoP stabilization

Light Touch improved the immediate sway response to the perturbation compared no touch (Table 2). As can be seen in Fig 4, participants showed lower intercepts independently of the type of stimulation. Post hoc analysis revealed a significant effect of block, which is the progression over all 12 blocks (Table 3).

Table 3. Results for analysis of gradual decrease.

Measure	P value						
	Stimulation Protocol F(1,238)	Light Touch F (1,238)	Block F (1,238)	Stimulation Protocol x Light Touch F(1,238)	Stimulation protocol x Block F(1,238)	Light Touch x Block F(1,238)	Stimulation protocol x Light Touch x Block F(1,238)
	Centre of Pressure						
Intercept	NS	< .001	< .05	NS	NS	NS	NS
Slope	NS	NS	NS	NS	NS	NS	NS
Constant	NS	< .001	< .001	NS	NS	NS	NS
	Tibialis Anterior						
EMG Integral	< .001	< .001	< .001	< .05	< .001	NS	NS
Peak Amplitude	< .001	< .001	< .001	< .05	< .05	NS	NS
	Gastrocnemius						
EMG Integral	< .05	NS	NS	NS	NS	NS	NS
Peak Amplitude	< .01	< .001	< .001	NS	NS	NS	NS
	Soleus						
EMG Integral	NS	NS	NS	NS	NS	NS	NS
Peak Amplitude	< .05	< .05	< .05	NS	NS	NS	NS

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The effect can be derived from Fig 4 as well, showing a gradual decrease over time. Additionally, stronger lateral push forces resulted in higher intercepts (Fig 5A).

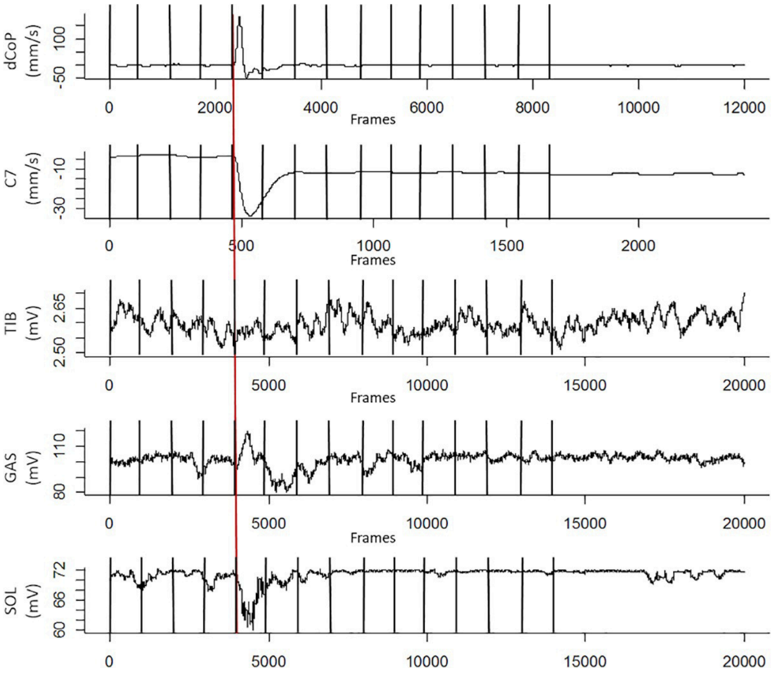

Fig 3. Illustrative data of one participant averaged time course over all conditions of sway (ML dCoP (mm/s)), the C7 marker (mm/s), and the muscle response of the Tibialis Anterior (mV), Gastrocnemius (mV) and Soleus (mV). The red line indicates the time of perturbation. Black vertical lines represent time bins of 1 second.

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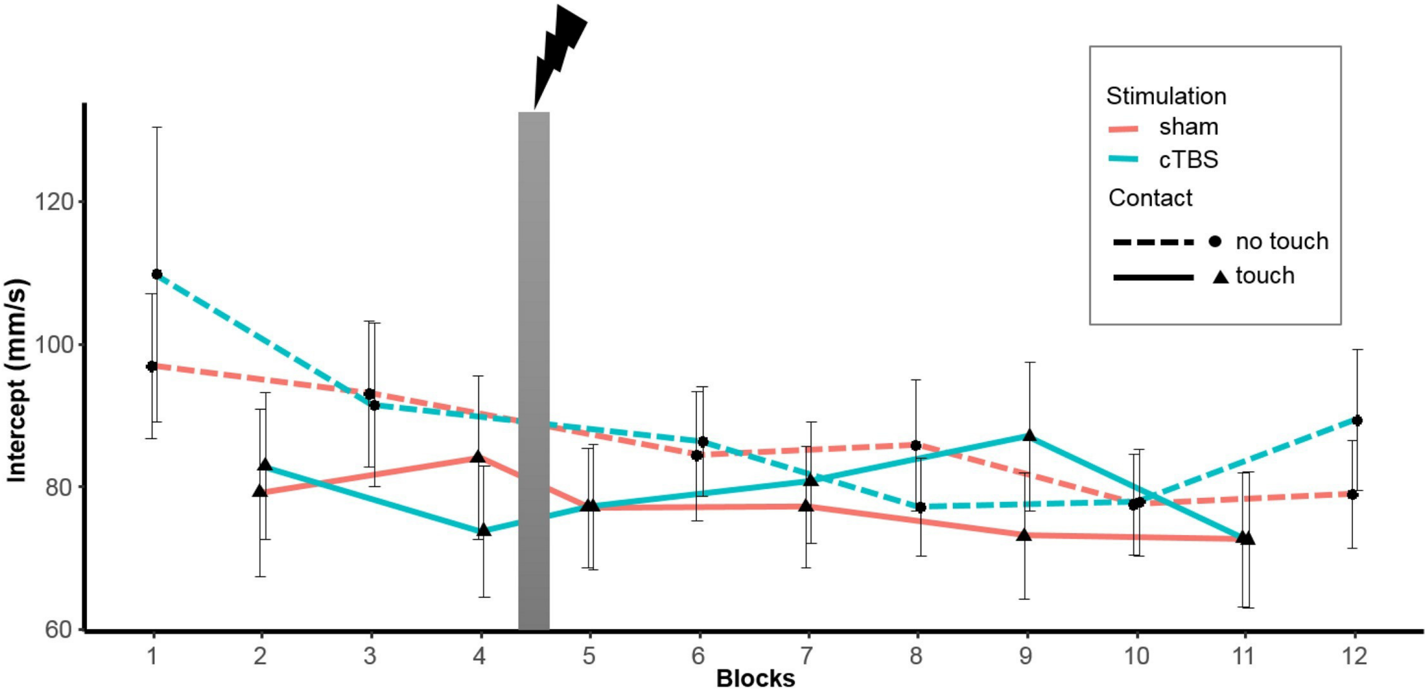

Fig 4. Progression of averaged intercept of the body sway at perturbation as a function of contact condition (Touch/No Touch) and stimulation protocol (sham/ cTBS). Wide grey vertical line represents stimulation (Blocks left to it are pre-test, blocks right to it are post-test). Error bars indicate standard error.

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The compensation time constant was only affected by push force. Similar to the immediate effect of the perturbation on sway, steady-state asymptote was reduced with Light Touch Independently of the type of stimulation (Table 2). Stronger pushing forces lead to a more variable postural steady state as indicated by higher asymptotes (Fig 5B). Asymptote showed a decrease of 15% in both the 1% and 7% force push condition and 20% decrease in the 4% force push

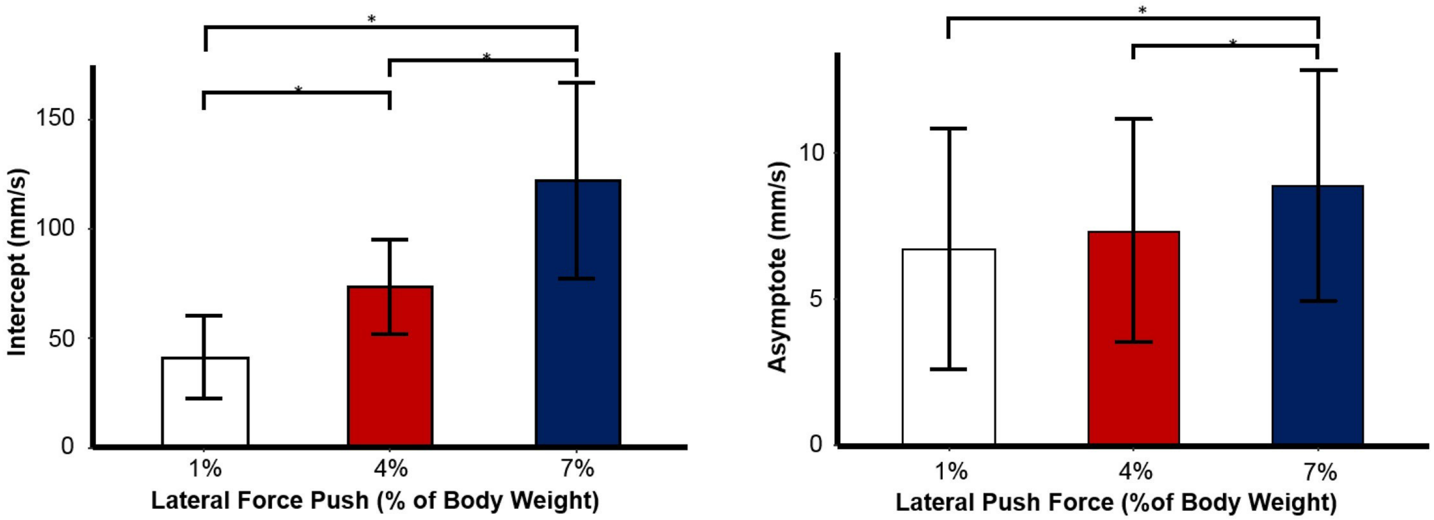

Fig 5. A) Averaged Intercept of the body sway at perturbation as a function of lateral push force (% of Body Weight). B) Averaged Asymptote of the body sway at perturbation as a function of lateral push force (% of Body Weight). Error bars indicate standard error.

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compared to the pre-test. In addition, the asymptote also showed an interaction between Light Touch and intra-session testing (Table 2). We see the highest value during no touch in the pre-test. Asymptote values decrease in the post test even without Light Touch. However, we also see that with Light Touch asymptote values are already decreased in the pre-test. Even though with Light Touch asymptote values do not decrease further compared to the pre-test, there is a significant difference between post-test levels (p = .003), with smaller asymptote values when utilizing Light Touch (Fig 6). Post hoc analysis revealed again a gradual decrease over time, independently whether Light Touch was established or not (p < .001) (Table 3).

EMG

Tibialis Anterior activity was affected by Light Touch and intra-session testing. Interactions between intra-session testing and stimulation protocol as well as between Light Touch and intra-session testing were found. General Tibialis Anterior activity decreased with the utilization of Light Touch. We saw that the highest level of general muscle activity (EMG integral) was expressed in the pre-test of the no touch condition, but decreased in the post-test. During the pre-test with Light Touch Tibialis Anterior activity already showed a lower level compared to no touch. Post hoc analysis of the two stimulation protocols revealed a significant effect of test (pre vs. post) for the Tibialis Anterior (p < .001) (Fig 7). Similar to the progression of sway we found gradual decrease of muscle activity over the progression of the 12 blocks (Figs 8 and 9). Post hoc test of the first four blocks before stimulation revealed no significant effect of stimulation session, showing that stimulation session is indeed an effect of the utilized stimulation rather than a general difference between sessions. Post hoc test did reveal a significant effect of Light Touch (p < .001) and Block (p < .05).

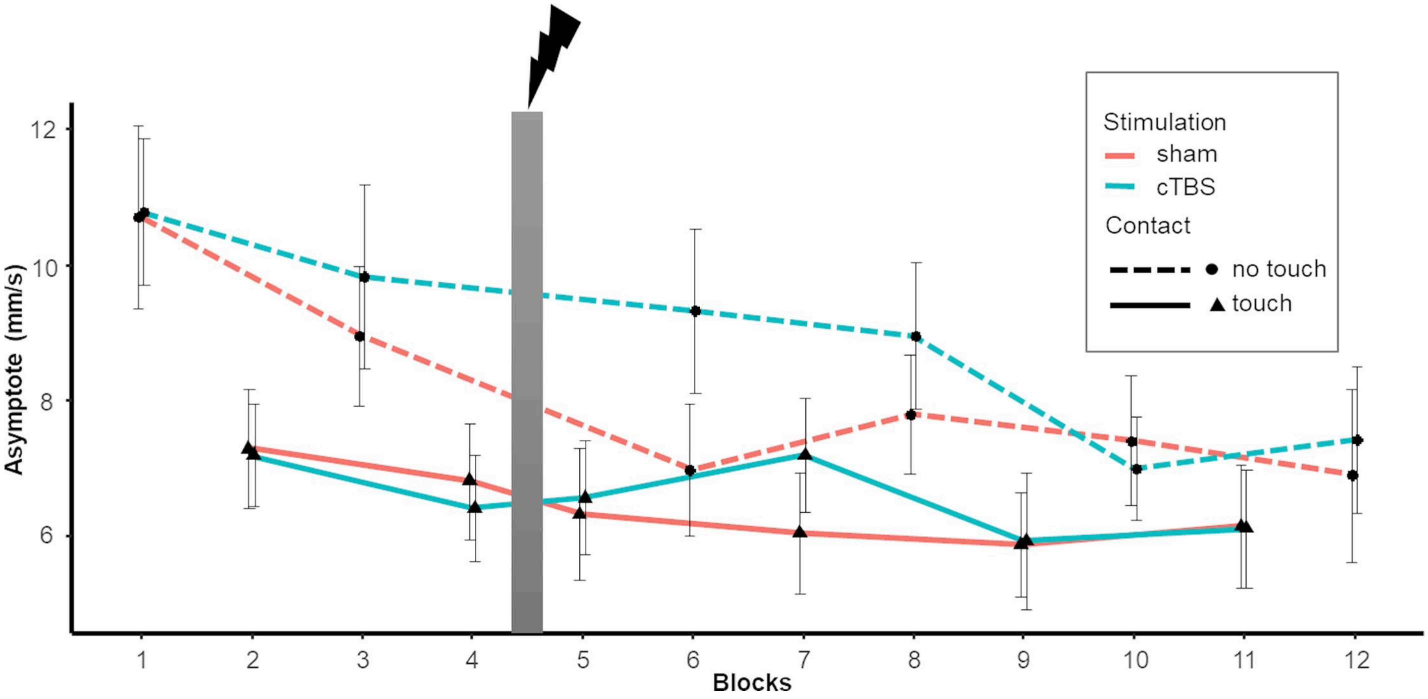

Fig 6. Progression of averaged asymptote of the body sway at perturbation as a function of contact condition (Touch/No Touch) and stimulation protocol (sham/cTBS). Wide grey vertical line represents stimulation (Blocks left to it are pre-test, blocks right to it are post-test). Error bars indicate standard error.

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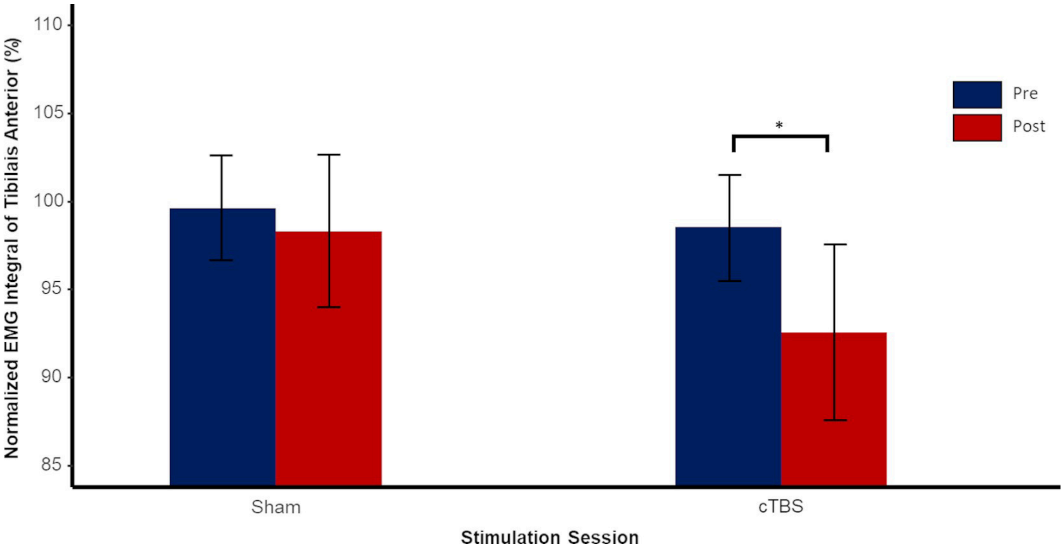

Fig 7. Normalized EMG Integral of Tibialis Anterior as a function of Test (Pre/Post) and stimulation protocol (sham/cTBS). Error bars indicate standard error.

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Looking at the decrease in percentages, we see that in the 1% and 7% force push condition EMG integral decreases 13% and 11% respectively, while the 4% force push condition shows a greater decrease with 16%. Interestingly, cTBS stimulation showed greater decreased levels of muscle activity of the Tibialis compared to sham. Following sham stimulation muscle activity is decreased by 11% but after cTBS we saw a decrease of 16%. As can be derived from Table 3 post hoc analysis showed a significant interaction of stimulation protocol and intra-session testing.

In terms of peak amplitude of muscle activity directly following the perturbation, Gastrocnemius, Tibilais and Soleus all showed lower peak activity amplitudes with Light Touch

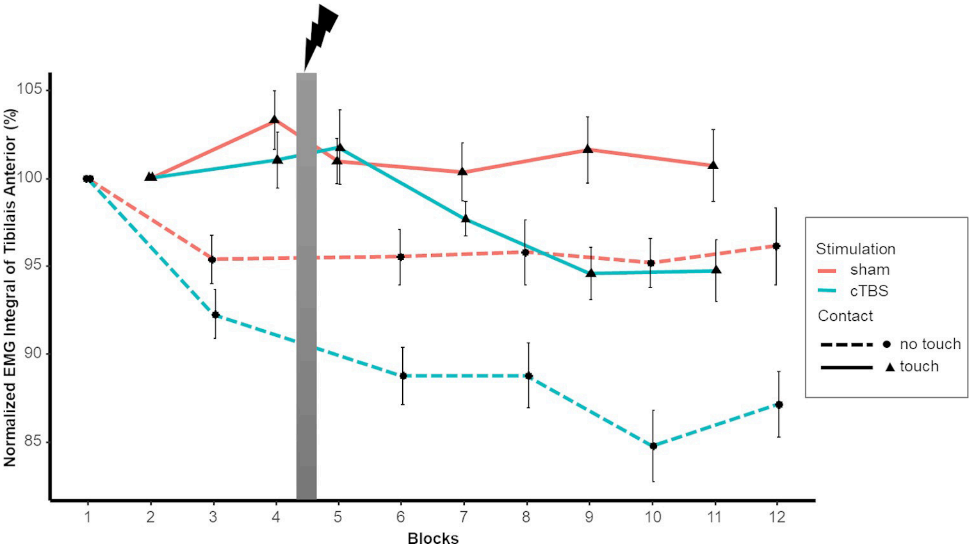

Fig 8. Normalized EMG Integral of Tibialis Anterior as a function of contact condition (Touch/No Touch) and stimulation protocol (sham/cTBS). Wide grey vertical line represents stimulation (Blocks left to it are pre-test, blocks right to it are post-test). Error bars indicate standard error.

https://doi.org/10.1371/journal.pone.0233988.g008

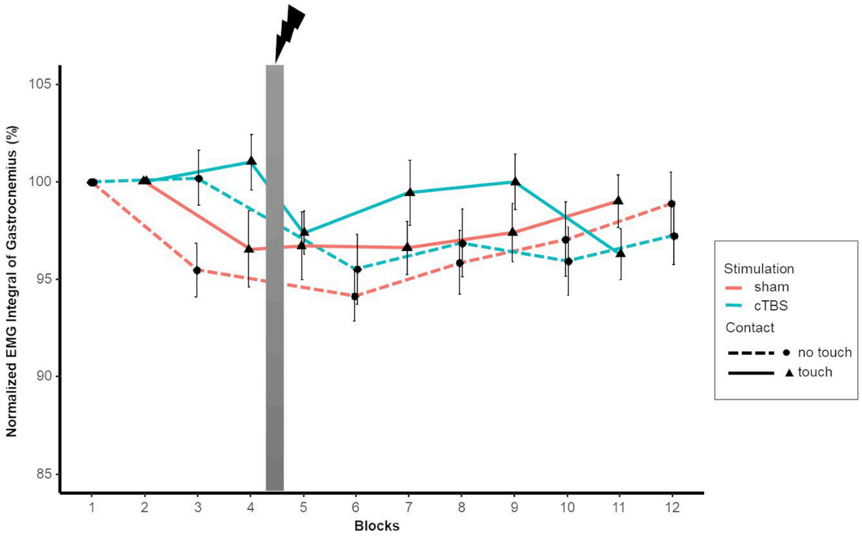

Fig 9. Normalized EMG Integral of Gastrocnemius as a function of contact condition (Touch/No Touch) and stimulation protocol (sham/cTBS). Wide grey vertical line represents stimulation (Blocks left to it are pre-test, blocks right to it are post-test). Error bars indicate standard error.

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compared to No Touch (Table 2). Finally, a significant interaction between stimulation protocol and intra-session testing was observed for peak amplitude of the Gastrocnemius. Post-hoc analysis showed a differences between stimulations protocols. There was a significant effect of test for Gastrocnemius $p < .01$ for the cTBS stimulation, while after sham no effects were found. Similar to the stimulation effects of the EMG integral, we see a decrease of peak activity after cTBS stimulation, while it stays the same after sham.

Discussion

Our study pursued two main objectives. The first was to investigate whether light fingertip contact improves balance compensation following a perturbation unpredictable in its relative force so that generation of a context-specific central postural set would be hindered. The second was to assess the role of the right posterior parietal cortex for the control of postural stiffness by disrupting the rPPC using continuous theta burst stimulation. We expected strong effects of light fingertip contact on body sway and muscle activations before, at and after a perturbation indicative of Light Touch feedback resulting in improved postural stability. Disruption of rPPC, on the other hand, was expected to hinder facilitation of sway stabilization with Light Touch but also affect the immediate response to a perturbation and sway stabilization by induced greater postural stiffness.

Facilitation of body sway control with light touch

Baseline sway before a perturbation was reduced by Light touch in line with previous studies assessing steady-state postural sway [1]. At the perturbation, Light Touch reduced the immediate response as well as the asymptotic post-perturbation steady state. In addition, activity of the Tibialis Anterior and Gastrocnemius was reduced with Light Touch. Similar results were found when investigating Light Touch benefits on balance stabilization following a sudden backward perturbation [5,6]. Light Touch led to smaller amplitudes of CoP displacement and decreased muscle activity of the Gastrocnemius. Martinelli et al. [5] argued that usually large body oscillations are prevented primarily through torque production around the ankles and that smaller displacement during Light Touch in return requires less muscle activation to produce smaller required correcting torque. Decreased general muscle activity (EMG Integral) in Tibialis Anterior across an entire perturbation trial agrees with this interpretation.

Against our expectations, Light Touch did not reduce the time constant of compensation following a perturbation. This observation contrasts with previous findings [4,5,6]. Johannsen and colleagues [4] observed shorter stabilization time constants with Light touch following both self-imposed as well as externally imposed perturbations. Similarly, Martinelli at al. [5] found reduced CoP sway during stabilization with Light Touch. However, their Light Touch effects for stabilization were limited to the most challenging conditions without vision while standing on a compliant surface. In all previous perturbation studies, that assessed the effect of augmented self-motion feedback with Light Touch, participants were tested in a normal bipedal stance posture with the perturbation in the antero-posterior direction [3,4,5,6]. In our present study, participants kept a tandem Romberg posture with a perturbation in the mediolateral direction. Failed generalization of the Light Touch benefit to the time constant of balance stabilization in the context of the present study could indicate that the benefits of Light Touch for active stabilization could be highly context-specific. A central postural set represents the sensorimotor context of a postural task including the available sensory channels and current mechanical constraints [24]. Stance with Light Touch will also resemble a specific central postural set adjusted to the current task requirements such as the inclusion of a specific spatial frame of reference centred at the contacting finger or the trunk depending on the task [25,26]. If the postural context involves a balance perturbation, the task set will also represent the anticipated consequences of a known perturbation as well as any appropriate postural responses. For example, exposure to a sequence of horizontal support-surface perturbations with the same amplitude and velocity results in an appropriately scaled initial response of the agonist muscle, in contrast randomizing perturbations with respect to amplitude and velocity will result in a default response, partly determined by the strength the preceding perturbation [27]. In our current study, participants had to alternate between central postural sets with and without finger Light Touch in blocks of six trials each. Within each block the sequence of the perturbation forces was randomized and therefore unpredictable in its magnitude. The absence of any indications of Light Touch facilitation of dynamic stabilization in the current study implies a distinction between context-invariant or context-sensitive elements of a central postural set. Context-sensitive or rate-of-change-dependent components, such as an adequate compensation strategy following a perturbation, might have been excluded from the Light Touch central postural set or alternatively were impossible to implement due to the unpredictability of the experienced perturbations. It should be noted here that we did not find a direct influence of Light Touch in terms of shorter stabilization of the time constants. However, participants with a lower intercept but a constant time constant would reach their steady state sway earlier. In this regard, it might be possible that a strategy that even further decreases the time constant was deemed redundant, given that participants already reached their steady state faster.

Disruption of the rPPC did not interfere with the processing of fingertip haptic feedback for the stabilization of body sway following a perturbation. This confirms our previous study, where we showed that disruption of the rPPC did not affect the integration and utilization of Light Touch in a quiet stance context [17]. The present study generalizes this observation to more dynamic postural contexts involving external perturbations. This leaves us with a conundrum as the rPPC has been considered an important brain area that represents peri-personal space [28] and performs coordination transformation processes for mapping local tactile stimulation into hand-centered, head-centered, or trunk-centered spatial frames of reference [29,30]. Thus it seems likely that disruption of the rPPC does not alter the postural effects of

Light Touch sensory augmentation. As for the reason why, it is possible that a central postural set for the control of body sway with Light Touch makes use of more limb-cantered body representations without involvement of a predominantly spatial reference frame or egocentric representation. Dolgilevica and colleagues [31] proposed a conceptual framework which emphasizes the role of body representations such as the postural configuration of the body as well as the size and shape of body segments in the spatial localization of touch. In a previous study, we observed effector-specific differences between participants' dominant and non-dominant hand in terms of sway after-effects following sudden removal of a Light Touch reference [32]. The after-effect, that is the time to return to no touch baseline sway, was prolonged when the dominant hand was used to keep the Light Touch contact. As our participants were all right-handed, the observation implies that involvement of the left-hemisphere delayed switching between sets by keeping the Light Touch central postural set active for longer [32]. Thus, the control of body sway with Light Touch but without visual feedback may rely more on representations of somatotopy in the secondary somatosensory cortex [33] than representations of external space in the posterior parietal cortex.

Control of postural stabilization following the perturbation

In our previous cTBS study involving a quiet stance situation, we found that disruption of the right PPC leads to a decrease of the general sway variability [17]. We attributed this reduction in sway to a disrupted process for the continuous exploration of the body's postural state [34] resulting in reduced inhibition of a process controlling postural stiffness [34]. Therefore, we expected that the postural perturbation paradigm of the present study would provide us with more direct evidence of an increase in postural stiffness following disruption of the rPPC. For example, reduced body sway in a steady postural state as well as a more rigid response to the lateral push, such as a reduced immediate effect of the perturbation on body sway but a prolonged time constant of stabilization, could be indicative of increased postural stiffness with reduced flexibility. The influence of postural stiffness on compensation of a balance perturbation has previously been shown by Horak and colleagues [35] testing Parkinson's patients, whose rigidity has been lowered by levodopa replacement therapy. Following support-surface translations these participants expressed less resistance and faster Centre-of-Mass displacement.

Jacobs and Horak [7] assumed that contextual cues of an impending perturbation are used to optimize anticipatory postural adjustments. Based on that assumption, Smith et al. [36] analysed the effects of support translations on anticipatory postural adjustments testing how different amplitudes of support surface translations in combination with different cuing conditions influences optimization of anticipatory postural adjustments. Displacement amplitude was either cued by means of repetitive, blocked perturbations, or a random sequences of displacement amplitudes of uncued perturbations was delivered. In the blocked sequences, CoP under the feet showed a slower initial displacement following perturbations as compared to the random sequences. The authors interpreted the result as supporting the notion that postural control is optimized when contextual cues are given prior to the perturbation. The exposure to similar perturbations across trials in a block, however, may have induced optimization of postural responses by adaptive motor control processes and not through contextual cues alone [36]. Coelho et al. [37] investigated whether optimized postural responses are a result of contextual cuing or whether they are dependent on motor experience. They were able to show that block sequence of perturbations leads to the generation of more stable automatic postural responses in comparison to the serial and random perturbation sequences. During block sequence perturbation lower body sway amplitude, decreased displacement velocity and longer delays of activation onset of leg distal muscles were found. They interpreted these results as optimized postural responses in the block sequence due to adaptive processes underlying repetitive perturbations over trials rather than to processing of contextual cues [37]. To better understand how the postural control system adjusts postural responses following a specific type of perturbation, Kim et al. [38] exposed participants to forward trunk pushes of 5 different strengths in randomized order and estimated the gradual scaling of the sensory feedback gain. After comparing the observed feedback gain scaling to perturbations expressed following support surface translations [39], they concluded that the postural control system seems to select a feedback gain set according to the current postural context as characterised by the type of a perturbation and biomechanical constraints. Although Kim et al. [38] favoured a feedback gain interpretation, they could not exclude the possibility of situation-specific changes in dynamic parameters such as joint stiffness and damping.

In our present study we found results indicative of an adaptive process in terms of lower leg muscle activity and steady state sway, with a general decrease over time, independently whether Light Touch was used or not. This supports the idea that exposing people repetitively to a perturbation leads to an optimization of the postural response. Interestingly, this adaptive process was present although participants were perturbed to a randomized sequence of three different force pushes within one block. Given the range of the perturbations with a small, medium and strong force push, one possibility is that instead of finding three strategies against the perturbation force, the postural control systems settled for a compromise across the three forces and prepared for a medium configuration. If this were the case we would expect to see greater improvement, respectively greater decrease of muscle activity and postural sway in the medium force push condition. Looking at the decrease in percentages, this was the case. While in the small and strong force push condition we see a reduction in the EMG integral of the Tibialis of 13% and 11% respectively, the medium force push condition shows the highest decrease with 16%. Similar results can be found for the asymptote, with a decrease of 15% in both the small and strong force push condition and 20% decrease in the medium force push.

Unexpectedly, cTBS stimulation resulted in more decreased levels of activity of the Tibialis anterior and peak activity of the Gastrocnemius compared to sham stimulation. This observation contrasts with tonic activity of the Gastrocnemius, where activity stayed relatively the same over time, independently of the type of stimulation. Sozzi and colleagues [40] investigated the individual role of the lower leg muscles during standing in tandem Romberg stance and reported roles of the muscles specific to individual balancing functions. They concluded that while the soleus supports the body against gravity, the Tibialis Anterior and the peroneus stabilize the body in the medio-lateral direction. This supports our conclusion that the greater reduction in Tibialis anterior activity is tied to an improved postural adaptation following cTBS of the rPPC.

The decrease of muscle activity in the Tibialis Anterior should not be mistaken as a direct influence of the rPPC disruption on muscle activity, but rather as a result of a centrally mediated adaptation of postural control to the challenges of a perturbation. If we assume that reduced lower leg muscle activity indicates an experience-dependent optimization of the postural adjustments, then we can conclude that rPPC disruption enhanced anticipation of the disturbing effects of the perturbation. In Kaulmann et al. [17], we argued that rPPC may be involved in a process with generates postural sway to actively explore the postural stability state, which might normally interact with a postural stiffness control process in a reciprocal inhibitory manner. Thus, cancellation or disruption of a process represented in the rPPC for exploring the postural state might lead to a clearer feedback-dependent signal used for the prediction of the effects of an externally imposed external perturbation and the optimization of any compensatory responses.

There is ample evidence, however, that points to the role of brain areas other than the cerebral cortex in the adjustment of postural responses to external perturbations of balance. For example, Thach and Bastian [41] reported that the cerebellum is involved in the adaptation of response magnitude, as well as in the tuning of the coordination of postural responses based on practice and knowledge. This was in line with Horak and Diener [42], who demonstrated that patients with cerebellar lesions are unable to scale the magnitude of their postural responses to predicable amplitudes of surface translations. Also involvement of the basal ganglia in postural responses following external perturbations as illustrated by Parkinson's disease resulting in the inability to modify postural responses to a perturbation [43]. For example, healthy subjects are able to change postural synergies immediately after a single exposure, while individuals with Parkinson's disease require several trials to adjust their responses [44]. Thus, we do not claim that the rPPC is exclusively involved in the adaptation to a postural perturbation but that the region nevertheless resembles an important component of a network of brain regions controlling postural stiffness and adaptation.

Limitations

We have no direct indicator of the neural effect induced by cTBS stimulation at the target cortical area. Therefore, we cannot assume without reservation that cTBS did indeed cause local inhibition of the rPPC as the region, being primarily involved in sensorimotor integration for movement control, does not project directly to end-effector specific areas in the primary motor cortex that could have validated its effectiveness. Therefore, the evidence presented by our study for a role of the rPPC in the adaptation of postural responses to unpredictable perturbations must be considered as circumstantial only. A subsequent study needs to follow-up our observations by being more properly designed to evaluate sensorimotor learning of the perturbations and which validates the disruption of rPPC by cTBS using a different probe task, for example assessing visual attention.

Conclusion

We found a strong effect of Light Touch, which resulted in improved stability following an unpredictable perturbation. Light Touch decreased the immediate sway response, as well as the steady state sway following re-stabilization. Decreased sway is accompanied by reduced muscle activity of the ankle Tibilais Anterior. We assume that the improved sway response lead to increased stability, which required less torque production around the ankles in order to stabilize the body. However, we did not find an improvement of the time constant in response to the perturbation with Light Touch. This contrasts with studies that investigated the benefit of Light Touch when compensating a perturbation in the sagittal plane, while standing in normal bipedal stance. The lack of improvement might be a result of a different postural context or the unpredictability of the force of the perturbations. We observed a gradual decrease of muscle activity, which is indicative of an adaptive process in terms of lower leg muscle activity, following exposure to repetitive trials of perturbations. This supports the idea that exposing people repetitively to a perturbation leads to an optimization of the postural response. Given the range of the perturbations we suspect that the postural control system settled for a compromise across the three different perturbation forces and prepared for a medium configuration. This is supported by the notion that we see greater decrease of muscle activity in the medium force push condition. Regarding the effects of the disruption of the rPPC we were not able to confirm our hypothesis that disruption of the rPPC leads to increased postural stiffness. However, we did find an unexpected effect of cTBS stimulation in terms of improvements of the aforementioned adaptive process. After disruption of the rPPC muscle activity of the Tibialis

Anterior is decreased even greater, compared to sham. From that we can conclude that rPPC disruption enhanced the intra-session adaptation to the disturbing effects of the perturbation.

Supporting information

S1 File.
(DOCX)

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Author Contributions

Conceptualization: David Kaulmann, Leif Johannsen.

Formal analysis: David Kaulmann.

Investigation: David Kaulmann, Matteo Saveriano.

Resources: Dongheui Lee, Joachim Hermsdörfer.

Supervision: Joachim Hermsdörfer, Leif Johannsen.

Writing – original draft: David Kaulmann.

Writing – review & editing: Leif Johannsen.

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4 Discussion

The goal of this dissertation was to identify the influence of cortical activity on light touch and how in contributes to the control of posture and balance. In order to do so, different experimental approaches have been utilized. On the one hand the working mechanisms of light touch have been explored and whether its effects are due to the additional sensory information form the fingertip or its suprapostural properties. Regarding the working mechanisms another study was carried out in order to investigate the timely properties of light touch, looking at the effects of intermittent light touch. The other string of research investigated the cortical correlates more closely. The effects of disrupting specific cortical areas on light touch and balance control was the main focus in these studies, investigating static, as well as dynamic situations. These studies revealed new insights into the light touch phenomenon, which will be discussed in more detail in the following pages. To do so, first the light touch effect itself will be discussed. Similarities and differences of the results in the four studies will be highlighted and put into context with recent findings from other studies. Following that, the role of the posterior parietal cortex will be examined more closely and what role it plays in the integration of light touch and the control of balance. In this regard it will also be discussed how the posterior parietal cortex is involved in the control of stiffness and compliance during postural control. Lastly, hemispheric specialization for light touch integration and postural control is discussed.

4.1 Light Touch

All studies incorporated in this dissertation were able to reproduce a light touch effect, similar to the one first mentioned by Jeka & Lackner (1994). In their study they found that a light haptic contact with the fingertip reduced postural sway. Given the light contact force of around 1N, this improvement cannot be attributed to a mechanical support but actually additional sensory information (Jeka & Lackner, 1994). Throughout the 4 studies presented in this dissertation, all confirmed this finding, showing improvement of postural control in both static and dynamic situations, when light touch was executed. In the first study it becomes apparent that longer light touch intervals lead to a greater effects of sway stabilization. A minimum of 2 seconds of light touch contact is required to show meaningful reductions of sway. Additionally, longer time periods of 10 seconds show a slight after effect, even after contact is removed. The second study was also able to show reduction of sway with light touch. Interestingly, the second study also showed that not only sensory information of the fingertip reduces body sway but that suprapostural task constraints are helping to reduce sway as well. It seems that both processes are active during light touch and able to modulate posture. The modulation of posture is not restricted to minimization of sway but also improves sway complexity, as has been shown by the third study. Decrease of sway variability was accompanied by an increased level of sway complexity, when light touch was utilized. Lastly the fourth study was able to show that light touch not only improves static quite stance but also improves sway response following unpredictable perturbations. With light touch immediate sway response following the perturbation, as well as steady-state sway was decreased. The striking similarity between these studies is the stabilization of sway variability during steady-state sway. Usually steady-state sway is achieved after standing quietly without any perturbation. This sheds light on two important findings. The first one is that light touch helps improve balance control during episodes of quite unperturbed stance, or once quite unperturbed stance is achieved. Even though experiments of this dissertation investigated different aspects of light touch, steady-state sway was assessed throughout all of them, making these findings comparable. As mentioned before, all four studies showed a reduction of sway variability during steady-state sway. Similar results were shown by Johannsen e al. (2014). They investigated the effects of 1Hz rTMS over the IPG with and without light touch. In their study passive touch was applied to the fingertip at random time intervals, with contact times ranging between 7 and 20 seconds. As the first study of this dissertation revealed, a touch contact of at least 2 seconds is necessary to induce behavioral changes, with longer time periods showing greater effects and a steady-state being achieved around 10 seconds of quite stance. Given the time range of Johannsen et al. it can me assumed that participants reached a steady-state during quite stance. Indeed, they found a reduction of steady-state sway, when light touch was established with an earth fixed reference point. Additionally, they found no effect of cortical inhibition by TMS. Steady-state sway was still improved by light touch after disruption of the IPG (Johannsen et al., 2014). This is in line with results from study III and IV of this dissertation. Both TMS studies showed that inhibition of the posterior parietal cortex did not alter integration of the haptic signal from the fingertips, with light touch remaining its stabilization properties. As to why alteration of cortical activity does not lead to a change in behavior will be discussed later on in this discussion.

This dissertation, together with the aforementioned study by Johannsen et al. shows strong evidence that light touch improves balance control once a steady-state of sway control is achieved. This might be connected to configurations from a central postural set. A central set allows descending commands to prepare sensory and motor systems for anticipated stimulus and task conditions (Schmidt et al., 1982). A central postural set is thus dependent on expectations, experience and task constraints, as well as sensory modalities. In this regard, quite stance with light touch will lead to a selection of a specific central postural set, adjusted to the current task requirements such as the inclusion of a specific spatial frame of reference centred at the contacting finger. Furthermore, suprapostural task constraints, such as maintaining only light haptic contact with a reference point, will also influence the selection of a postural set, guaranteeing that the specified task gaol is fulfilled. As I was able to show in the second study, benefits of light touch are not solemnly due to the additional sensory information, but also influenced by the suprapostural nature of the haptic task. Given that general task goal and constraints of the postural context influence the selection postural sets, it seems highly probable that suprapostural tasks impose similar selection processes.

However, regarding the sensory contribution to balance control of light touch it seems more reasonable of the CNS to select a postural set that relies on haptic information only after the likelihood is high that the haptic channel will provide reliable feedback for an extended period. Once such a state has been achieved it also seems reasonable to keep this set active. This view is supported by the notion of sensory re-weighting. During postural control information from the different sensory systems is constantly evaluated in order to update the internal body schema. Depending on the situation however, one sensory source might become unreliable or less important and in return will be weighted less for providing information about the body's postural state (Kandel, 2013). For example, if people walk in the dark, the visual information will be regarded less useful, while somatosensory information form the soles will be weighted as more useful for updating the body schema and the body's orientation in space. This might explain why we see such strong effects of light touch in all 4 studies once a steady-state of sway is achieved, since only then is the system fully utilizing the additional haptic information from the fingertips. Only after light touch has been providing reliable information for a longer period of time is a postural set selected, that relies on a heavier weighting of this specific sensory modality.

The second important finding regarding light touch in this dissertation is the wide spread additional benefits. As the four studies were able to show, these benefits are not restricted to improvement of sway variability during steady-state sway. Moreover, we see various effects of light touch, providing evidence for its effectiveness in a variety of situations. These effects are highly task and context specific. The first study was able to show that longer periods of light touch can lead to small after effects, even after removal of fingertip contact. In the second study results reveal that light touch can be utilized in order to fulfill a suprapostural task, by minimizing sway, making a visual task more successful. The fourth study then showed that light touch can contribute and improve compensation responses following perturbations. These results cannot be generalized over all four studies but demonstrate the high versatility of light touch towards improvement of balance control. This is further supported by numerous studies applying light touch in varying situations, such as walking. Forero et al. (2013) were able to show that light touch provides sensory cues, which can even help stabilizing the body while walking and contribute to corrective reactions initiated by balance disturbances encountered during walking. This is further supported by studies showing that light touch reduces medio-lateral sway variability during walking (Kodesh et al. 2014; Oates et al. 2017). Furthermore, multiple studies were able to show the effectiveness and usefulness of light touch for different patient populations. For example, Dickstein et al. (2003) showed that somatosensory substitution from a cane in the hand could be used to improve the magnitude of medium latency postural responses to slips and trips in patients with diabetic neuropathy. Another study by Rabin et al. (2013) investigated the effects of light touch in Parkinson’s disease. They found that, haptic cues from manual contact improved balance control in individuals with Parkinson’s disease, even when contact was not sufficient to provide mechanical support. Balance impaired patients suffering from bilateral vestibular loss also benefit from light touch, as Lackner et al. (1999) were able to show. The vestibular loss subjects were significantly more stable with light touch of the index finger. They also swayed less with sight and touch than just sight. What can be derived from these studies, as well as experimental finding of this dissertation, is that light touch has varying effects depending on the context and the population. However, all studies find positive effects of light touch for the control of balance and posture. This dissertation together with numerous other studies shows that even though we do not fully understand light touch in all its intricate details, it is a useful and effective strategy to improve balance control. As mentioned in the introduction earlier, a superior way to manage fall prevention would be a technique that stabilizes balance impaired people but at the same time challenges them enough to prevent coordination from deteriorating. Light touch and its high versatility makes it a great strategy for balance impaired populations to utilize in their daily living, in order to improve balance control and reduce risk of falling. Instead of relying on walking aids too early, light touch might be a good alternative for non-severe cases to maintain independency for longer period of time.

4.2 Posterior Parietal Cortex

The second goal of this dissertation was to identify the role of involved cortical areas, mainly the role of the posterior parietal cortex for the integration of light touch. It should be noted that the posterior parietal cortex is primarily mentioned in the literature being associated with visuomotor coordination as well as spatial attention. However, there is evidence showing that the PPC is further involved in the integration of light touch, as well as reactive balance control. An et al. (2019) investigated the contribution of the sensory motor cortex and the PPC to recovery responses following unpredictable perturbations during standing or walking. Both areas showed a suppressed activity in the alpha band during periods of balance recovery. The role of the PPC is further supported by reports showing that lesions in the posterior parietal cortex following stroke lead to reactive postural control deficit, such as impaired recruitment of paretic leg muscles and a more frequent occurrence of compensatory muscle activation patterns compared to controls. The researchers concluded that the PPC is part of a neural circuitry involved in reactive postural control in response to lateral perturbations (Lin et al., 2014). Furthermore, there are studies providing evidence for the involvement of the posterior parietal cortex during light touch. Ishigaki et al. (2016) performed an EEG study and were able to show activity in the posterior parietal cortex when light touch was initiated. They found increased high-alpha TRPD in two electrodes (C3, P3), but only when acquiring a stable external reference with the fingertip. These two electrodes respond to the primary sensorimotor cortex and the left posterior parietal cortex. In a follow-up study they investigated the effects of tDCS over the left PPC on the light touch effect. They showed cathodal tDCS of left PPC increased RMS in the medio-lateral direction and attenuated the LT effect in the medio-lateral direction at the postcathodal tDCS, when touching a fixed point with the right fingertip (Ishigaki et al., 2016). As mentioned earlier Johannsen et al. (2014) investigated how rTMS over the left inferior parietal gyrus (IPG) influences sensory re-organization for the control of postural sway with light fingertip contact. They reported that rTMS over the left IPG reduced overshoot of sway after contact removal. This result indicates that this brain region may play a role in inter-sensory conflict resolution and adjustment of a central postural set for sway control with contralateral fingertip contact. These studies taken together suggest the influence of the PPC for balance control, as well as light touch, which makes it a great candidate to further investigate its role for the control of both mechanisms. Using continuous Theta Burst Stimulation (cTBS) I investigated the effects of inhibition of either the left or right posterior parietal cortex. However, no stimulation effects regarding the integration of light touch were found, independent from the stimulation side. After disruption of either area, light touch was still integrated correctly and improved stabilization of sway. Usually it would be expected that integration of the touch signal is disturbed contralateral to the disrupted side. No diminishing effects contralateral or ipsilateral have been found in study III (Kaulmann et al., 2017). Interestingly, there was a general reduction of sway after stimulation of the right posterior parietal cortex, but not after stimulation of the left posterior parietal cortex. This reduction in sway was accompanied by a reduction in sway complexity as shown by the DFA. These combined observations may indicate increased postural stiffness. Increased stiffness could be the result of lowered inhibition of stiffness control by a disrupted process, which actively explores the body's stability state and therefore opposes stiffness. Increased stiffness might reduce the body's ability to react to unforeseen perturbation, due to a lack of flexibility. Results were followed up with a study looking at the effects of inhibition of the rPPC in a dynamic situation. Again, disruption of the rPPC did not interfere with the processing of fingertip haptic feedback for the stabilization of body sway following a perturbation (Kaulman et al., 2020). This confirms the finding form the previous study and extents it towards a more dynamic postural context.

This is insofar problematic as the rPPC has been considered an important brain area that represents peri-personal space (di Pellegrino et al., 2015) and performs coordination transformation processes for mapping local tactile stimulation into hand-centered, head-centered, or trunk-centered spatial frames of reference (Heed et al., 2015; Ruzzoli et al., 2014). The answer to this discrepancy might lie in the aforementioned configuration of a postural set. It is possible that a central postural set for the control of body sway that utilized haptic feedback from the fingertip uses a more limb-centered body representation without involvement of a predominantly spatial reference frame or egocentric representation. Thus, the control of body sway with light touch but without visual feedback may rely more on representations of somatotopy information in the secondary somatosensory cortex, rather than representations of external space in the posterior parietal cortex. Additionally, regions in the cerebellum and the brain stem have been identified to be involved in the process of sensory integration. For example, the spinocerebellum receives signals from rapidly conducting proprioceptive and continues fibres, while vestibular nuclei and reticular formation receive sensory input from slowly conducting somatosensory fibres (Kandel, 2013). Given this wide spread involvement of different cortical areas for the processing and integration of sensory information, it seems plausible that disruption of PPC alone is not able to induce any changes. However, it should be noted here, that another reason for a missing effect of cTBS disruption might be simply due to a failed stimulation. There is no direct indication for the neural effect induced by cTBS stimulation at the target cortical area. However, the PPC as such is primarily involved in sensorimotor integration for movement control and does not project directly to an end-effector, which could have been checked for inhibitory effectiveness. Another possibility for a non-existent effect of TMS disruption might be due to the neuroplasticity and interhemispheric cooperation of the brain. There is a number of studies of patients suffering from unilateral stroke, suggesting that the contralateral, non-affected hemisphere shows plastic changes in its activity level, trying to compensate for the loss of function (Netz et al., 1997). It seems unlikely that these axon collaterals developed after stroke. However, they might exist prior to the stroke, being usually inhibited by interhemispheric inhibition. After a stroke, due to lack of inhibition, these connections may then become unmasked (Netz et al., 1997). The cTBS protocol might have simulated a lesion-like inhibition of cortical activity in one hemisphere, leading to an activation of these pre-existing pathways. In return the, the non-affected hemisphere tried to take over the function of the affected cortical area. In both cTBS studies, only one area at a time was inhibited, possibly enabling the other hemisphere to compensate the loss of function. Future studies should follow up on the question whether inhibition of both the rPPC and lPPC simultaneously induce any changes towards the integration of light touch. Even though I was not able to show that inhibition of either the left or right PPC influence integration of light touch, I was able to show that especially stroke patients suffering from a lesion in either of them, could still benefit from light touch for balance stabilization in static and dynamic situations.

4.3 Stiffness Control

The third objective of this dissertation was to assess the role of stiffness control towards balance and how it is modulated by light touch. Study III of this dissertation found a general decrease of sway variability after disruption of the right PPC. This effect was complemented by a decrease in sway complexity, in terms of a change from a correlated to a non-stationary signal. Together these observations may indicate increased postural stiffness. An increase in stiffness could have been the result of lowered inhibition of stiffness control by a disrupted process, which actively explores the body's stability state and therefore opposes stiffness (Kaulmann et al., 2017). Stiffness is an integral part of balance control. Biomechanical properties of the tendons and muscles provide inherent stiffness constraints that already help stabilize standing balance. However, these passive constraints are not enough to stabilize the body on its own. Previous studies by Winter et al. (1998) and Morasso & Schieppati (1999) calculated that around 200% of gravitational toppling torque is required to stabilize postural sway and prevent the body from losing balance. Sakanaka & Reynolds (2016) calculated passive stiffness ranging between of 31% to 78%. This is in line with other studies calculating passive stiffness up to 91% toppling torque (Loram & Lakie, 2002). These results provide evidence that passive stiffness is present and integral of the control of posture. However, passive stiffness alone is not able to stabilize standing balance. This leads to the assumption that there is active modulation involved in the production of postural stiffness. In this regard, Sakanaka & Reynold (2016) found in their study that in those subjects that expressed less stiffness, postural sway was higher. They suggest that less stiffness might be an indicator for less stability. However, they also mention that these results are limited to smaller perturbations and that it remains unclear what these changes of stiffness implicate for larger perturbations. A recent study by Pretty et al. (2019) revealed that increased trunk and hip stiffness during reactive stepping resulted in greater CoM displacement, increasing the likelihood of loss of stability. This supports the notion that there is an optimal level of stiffness during postural control, which is intermediated by two processes, that usually remain in an equilibrium (Kaulmann et al, 2017). These two processes are responsible for control of stiffness on the one hand, and actively exploring the own body’s current state of balance in the context of a specific postural configuration and orientation on the other (Riccio et al., 1992). The results from study III suggested that disruption of the rPPC led to increased postural stiffness, which decreased sway variability and complexity. It was hypothesised that this would result in a worsened balance control, making it harder for people to react to unforeseen perturbations (Kaulmann et al, 2017). However, results from study IV revealed no effect of rPPC disruption on balance compensation following a perturbation (Kaulmann et al., 2020). As to why I was not able to confirm the hypothesis is closely related to the arguments presented in the previous paragraph regarding the PPC. The first one being the possibility that cTBS over the rPPC failed, thus not introducing increased postural stiffness. However, given that study IV found behavioural changes after cTBS compared to sham in regards to the general muscle activity of the Tibialis Anterior, it seems unlikely that no cortical activity changes occurred. The second reason is related to the aforementioned influence of existing postural sets. In the last study participants did not knew how strong the perturbation will be, however they were aware that a perturbation will be executed every trial. Given that experience and anticipation play a great role in the selection process of postural sets, it seems likely that participants selected a postural set fit for this specific situation. In contrast, being expected to stand only in quite stance without perturbation, as in study III, led to a selection of a different postural set. Keeping these points in mind, it can be speculated that depending on the selected postural set disruption of the rPPC led to different behavioural changes in these two distinct situations.

4.4 Hemispheric specialization in the context of postural control

The discussion in the previous paragraphs made clear that the involved network of different cortical areas for the integration of light touch and postural control cannot be determined that easily. Many of our assumption regarding the experimental design were based on the notion of hemispheric specialization. Indeed, for many abilities such functional specialization has been proven to be correct. Most famous Paul Bronca and Carl Wernicke were able to show that language is impaired following damage of the left inferior frontal gyrus, and the left superior and middle gyri. Further research in lateralization of cortical functions led to the idea of hemispheric specialization, with the left hemisphere being predominantly involved in linguistic abilities skilled movement and the right hemisphere in visuospatial functions (Serrien et al., 2006). Much focus has been invested in investigating this sort of functional specialization. What has been slightly ignored is the mechanism of functional integration, which is the process of interaction and cooperation between specialized neural regions, in order to fulfil specific tasks (Friston et al., 2005). The results from this dissertation provide further evidence of such a process and its vital role in postural control.

Study I revealed a slight benefit of light touch when using the dominant hand, with a less prominent overshoot after touch removal (Kaulmann et al., 2017). This finding supported the notion of an influence of handedness for the utilization of light touch. Meaning that when using the dominate hand, light touch will be more effective. The concept of handedness is closely related to hemispheric specialization, since studies identified that control of one hand is organized in the contralateral hemisphere (Serrien et al., 2006). This is insofar important as it was expected in the study III that disruption of the PPC in one hemisphere would result in diminished effect of light touch contralateral to the disrupted side. First of all, in that study I was able to show that there were no differences between hands, independent of handedness. Both left and right handed participants were able to use either hand equally effective for postural control (Kaulmann et al., 2017). This provides evidence against the influence of handedness on light touch. More interestingly, I was not able to find any effects of disruption in regard to light touch integration (Kaulmann et al., 2017). As mentioned earlier, this might be due to the interhemispheric cooperation. In other words, after inhibition of the PPC in one hemisphere sensory integration of the light touch signal has been performed by the PPC in the ipsilateral hemisphere of the used hand. Such plastic changes in activity levels, trying to compensate for the loss of function have been observed previously (Netz et al., 1997). Following stroke and a loss of interhemispheric inhibition, prior existing pathways might be activated to enable other cortical areas to take over the functional role of the disrupted area (Netz et al., 1997).

Hemispheric asymmetries are not only found in handedness, but also for a wider set of movements. General speaking it has been postulated that the left hemisphere is predominantly controlling open-loop movements, while the right hemisphere controls closed-loop movements, which are dependant of sensory feedback (Haaland et al., 1989; Serrien et al., 2006). Postural control as such would fall under the functional role of the right hemisphere. As proposed by Sainburg et al. (2002), the left hemisphere is primarily involved in the control of limb trajectories, while the right hemisphere primarily control limb position and posture (Serrien et al., 2006). That the right hemisphere is heavily involved in postural control is supported by results from study III. After inhibition of the PPC in the right hemisphere we see a general effect in balance control expressed by a change in body sway. Sway variability, as well as sway complexity is reduced compared to sham or inhibition of the left PPC. This reduction was interpreted as a decline in performance of balance control. It was that this decrease of sway variability in combination with the decrease in sway complexity was a result of increased postural stiffness, which lead to a decline in the performance of balance control. In order to explain this increase in postural stiffness we postulated a model in which the right PPC is involved in a process of active exploration of sway, in order to gain information about the postural state. This process is usually in equilibrium with a second process, which controls active stiffness modulation. As a result of inhibition of the right PPC the process of active exploration was disrupted, altering the equilibrium state and leading to an increase in postural stiffness (Kaulmann et al., 2017). The involvement of the right PPC in such a process would support the idea of hemispheric specialization, with the right hemisphere being primarily involved in postural control. However, as results from study IV revealed, such a distinction might be not as strict as it seems. It was expected that increased stiffness, resulting from inhibition of the right PPC would result in a less flexible and thus worse balance response following a perturbation. However, no effects regarding the compensation response or any other balance related performance decline after disruption of the right PPC were found. Furthermore, there was no evidence of increase postural stiffness as in the previous study (Kaulmann et al., 2020). The question arises why inhibition of the right PPC in one situation leads to a decline of balance performance but not in the other situation. If we follow the argument of hemispheric and functional specialization inhibition of the right PPC in both the static and dynamic situation should result in the same changes. However, if we consider the process of functional integration these seemingly contradictory results make more sense. During a complicated task such as maintaining posture a network of multiple cortical areas has to communicate in order to fulfil the task. As discussed earlier in the context of postural sets, factors such as experience, expectation, attention and task goal have an influence on postural control (Schmidt et al., 1982). This of course means that areas involved in these processes will have to communicate at some point and depending on the task requirements and involved cortical areas this communication will likely differ as well. Furthermore, Johansen-Berg et al. (2002) were able to show that after injury, cortical regions associated with bilateral control Ftake on enhanced motor processing responsibilities, which supports the idea that cortical areas can assume functional roles of damaged cortical regions (Sierren et al., 2006). Taken all together, it seems that the asymmetrical functional distinction is not as strict as previously thought but that hemispheric contribution to postural control is actually more dynamic and may change depending on task requirements and environmental characteristics.

4.5 Limitations

The limitations in this dissertation are mainly related to the cTBS stimulation and the perturbation paradigm. Regarding the cTBS protocol I have no direct measurement of the neural effect induced by cTBS stimulation at the target cortical area and whether cortical activity was indeed inhibited. However, this lack of control is also due to the nature of the target region. The PPC is primarily involved in sensorimotor integration for movement control and does not project directly to an end-effector. Another limitation in my stimulation protocol was that the PPC was only stimulated unilaterally, which might have caused interhemispheric compensation, leading to a lack of disruption effect for haptic feedback integration. The third limitation is related to the perturbation paradigm in the fourth study. Even though participants were not able to predict intensity of the perturbation, they were still aware that a perturbation will be executed. This might have led to the selection of a different postural set, compared to the previous study, which in return influenced behaviour towards the perturbation.

4.6 Outlook

Future studies focusing on integration of light touch should incorporate not only the of use unilateral stimulation protocols, but stimulate target areas in both hemispheres as well. Furthermore, it would be interesting to investigate stimulation protocol that facilitate cortical activity rather than inhibit it, in order to gain insights into the relationship between cortical activity levels and light touch integration. Future perturbation studies should also try to improve unpredictability of perturbation stimuli. Making perturbations as unpredictable as possible will prevent participants from being too rigid in their strategy selection. This might be achieved by not only altering the time of perturbation and its intensity, but also by introducing trials throughout the experimental session that do not have any perturbation stimulus. Lastly future study should always keep in mind that cortical activity, Light Touch and postural strategies are heavily interlinked and are influencing each other.

Conclusion

This dissertation tried to elucidate working mechanisms of light touch and which cortical activity contributes to the processing and integration of light touch for the stabilization of balance. Results from four different studies confirm and extend previous findings of the light touch phenomenon. Regarding the working mechanisms of light touch, it became apparent that the duration of haptic contact is of great importance and influences the effectiveness of light touch. Durations have to be longer than 2 seconds in order for the haptic feedback to become relevant and be utilized by the CNS for the stabilization of balance. Longer touch durations yielded greater improvements, even showing after-effects after removal of the haptic contact, when this contact was longer than 10 seconds. Interestingly, these effects were only observed when established with the dominant hand, providing evidence for hemispheric lateralization. There seems to be a faster consolidation of a postural set that utilizes light touch, when this tactile feedback is processed in the dominant hemisphere. The second interesting insight into the working mechanisms of Light Touch is that sensory feedback alone is not the only contributing factor to the effect of Light Touch. Moreover, suprapostural task constraints, mainly the instruction of maintaining only light haptic contact, helps to minimize body sway variability. Both aspects do not work exclusively but cooperatively to reduce body sway in order to help fulfil a specific task goal.

Another important finding is the importance of light touch for the stabilization of steady-state sway. Throughout all four studies light touch showed a reduction of sway variability during steady state sway. This goes back to the first study, showing that longer touch durations lead to greater improvements. This is related to the existence of postural sets, which are based on situational circumstances, task goals, experience, current mental state, etc. and help selecting fitting strategies to maintain balance. The longer the haptic contact is kept, the more relevant it becomes for the stabilization, since it constantly generates additional sensory feedback about the body’s postural state. In order to account for the heavier weighted haptic sensory feedback, a postural set that makes more use of that feedback is selected, thus elevating the light touch effect. In other words, the availability and reliability of a haptic signal leads to the selection of a different postural set, that incorporates the sensory information even better, resulting in improved postural stabilization.

The second objective of this dissertation was to elucidate the relationship of cortical activity and the integration of light touch for the control of balance. The hypothesis that alteration of activity in the PPC, an area likely involved in the integration of haptic sensory information, would lead to a disappearance of the effect of light touch on balance control proved to be incorrect. After cTBS application over the PPC, sensory information form the fingertips was still correctly integrated and utilized to improve body sway. The reason why no stimulation effect was apparent has multiple implications. The most obvious one being that the PPC is the wrong cortical area to disrupt when looking at sensory integration of a haptic signal. However, one should not be too quick disregarding the possibility that the PPC plays a role and that cTBS application indeed altered cortical activity. Another possible explanation for a lack of stimulation effect might be related to hemispheric lateralization and interhemispheric cooperation. Axon collaterals might have activated the corresponding brain are in the non-affected hemisphere to take over the function of the altered cortical area. Given that disruption of the PPC was only unilateral, meaning either left or right PPC but never simultaneously, it might be possible that the non-disrupted PPC compensated the loss of function of the disrupted PPC. In that case cortical activity was altered in the target area, but due to compensation measurements of the cortical network integration of the haptic signal was still possible. This evidence suggests that lateral specialization is not as strict but can be modulated more dynamically by interhemispheric cooperation. Lastly, it is possible that the observed effects of light touch were due to the suprapostural aspects. Given that both mechanisms, the sensory feedback loop and the suprapostural task constraints play a role in minimizing sway, it is plausible that the stimulation indeed caused failed sensory integration, but due to the suprapostural task constraints sway was still being minimized.

Even though there is no apparent stimulation effect on light touch, results showed an effect on balance control directly. Disruption of the rPPC during quite stance showed decreased sway variability, as well as decreased sway complexity, which might be indicative of increased postural stiffness. However, in the follow-up study such an effect could not be observed during the more dynamic situation of a perturbation paradigm. Nevertheless, a different stimulation effect was found, affecting general muscle activity of the Tibialis Anterior. These results suggest a greater role of the PPC for general balance control. The differences in behavioural changes following cTBS might be the result of different postural strategies the arise when facing a dynamic context compared to a static one. Given what is known and was discussed earlier about postural sets it seems plausible that a different postural set is selected when being required to stand quite, compared to expecting and needing to compensate for a perturbation. Hence, what results in a specific stimulation effect during one active postural set, results in a different behavioural change during a different postural set.

This dissertation exposed an interesting relationship between light touch, postural sets and cortical activity. It becomes apparent that these three aspects are closely interlinked in regards to balance control and influence each other. The availability of light touch leads to the selection of a different postural set, which in return influence effectiveness of light touch integration, which is influenced by cortical processes and vice-versa. These cortical processes are highly adaptable and can be modulated dynamically by the CNS, in order to ensure that loss of function is compensated by other cortical areas. It is thus very important to keep these aspects in mind when investigating balance control. Nevertheless, this dissertation was able to show the effectiveness and versatility of light touch for control of balance and posture. In regards to fall prevention and rehabilitation a superior way to manage these aspects would be a technique that supports balance impaired people in their ability to control balance, but at the same time challenges them enough to prevent further loss of coordination. Light touch proves to be a great strategy for balance impaired populations to utilize in their daily living, in order to improve balance control and reduce risk of falling. Instead of relying on walking aids too early, light touch might be a good alternative for non-severe cases to maintain independency for longer period of time.

List of Abbreviations

CoM – Center of Mass

BoS – Boundary of Support

CNS – Central Nervous Sytsem

CoP – Centre of Pressure

TMS – Transcranial Magnetic Stimulation

rTMS – repetitive Transcranial Magnetic Stimulation

IPG – Inferior Parietal Gyrus

S1 – Sensory Motor Cortex

SMA – Supplemetery Motor Area

PM – Premotor Area

M1 – Primary Motor Cortex

LT – Light Touch

N – Newton

MFG – Middle Frontal Gyrus

ML – Medio-lateral

Hz – Hertz

s – seconds

EMG – Electromyography

cTBS – continuous Theta Burst Stimulation

MEP – Motor Evoked Potentials

MNI – Montreal Neurological Institute

SPL – Superior Parietal Lobule

IPS Intraparietal Sulcus

VSDT – Visual Signal Detection Task

IFC – Implicit Feedback Coupling

LTT-IJ – LT with independent jitter

LT-CF – LT with jitter depending on LT contact force

LT-BS – LT with jitter depending on body sway

NT-BS – no contact with jitter depending on body sway

PPC – Posterior Parietal Cortex

rPPC – right Posterior Parietal Cortex

lPPC – left Posterior Parietal Cortex

DFA – Detrended Fluctuation Analysis

tDCS – transcranial Direct Current Stimulation

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Statutory Declaration/ Affidavit

I hereby confirm that the dissertation “Cortical Cortical processing of light touch for the control of postural stability” is the result of my own work and that I have only used sources or materials listed and specified in the dissertation.

17.07.2020

David Kaulmann