

Central Mechanisms underlying Tactile Suppression

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Abstract

Tactile sensations on a moving limb and the neural responses associated with them are suppressed. This phenomenon has often been described as a general reduction in somatosensory processing during movement. However, converging evidence instead supports a more selective form of sensory gain control shaped by central predictive mechanisms and motor context. Using psychophysics, electroencephalography (EEG), and kinematic analyses, this thesis examines how precise sensorimotor predictions shape tactile suppression and how tactile sensitivity and cortical processing vary with feedback demands during goal-directed reaching.

First, I demonstrate that suppression of external vibrotactile probes during motor planning is tuned to specific sensorimotor predictions. Next, I characterize somatosensory evoked potentials (SEPs) to naturalistic high-frequency vibrotactile stimulation, addressing a gap in the EEG literature that has predominantly relied on electrical nerve stimulation. I quantify how SEP amplitudes scale with vibration intensity and compare vibrotactile with electrical stimulation, revealing distinct early processing for both modalities. Using this naturalistic stimulation paradigm, I then show that tactile suppression and early cortical gating follow the same temporal pattern across a goal-directed reaching movement. This pattern indicates that tactile processing during complex movements reflects state-dependent feedback demands.

Together, these findings characterize tactile suppression and gating as flexible, precise forms of predictive sensory gain control at early stages of sensorimotor integration, likely mediated by cortical and corticospinal circuits. In this view, tactile suppression reflects the behavioral expression of sensory gain regulation, through which central control shapes the influence of somatosensory signals on movement.

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I Synopsis

1 Introduction

After washing the dishes, I reached for a fresh tea towel from its usual spot by the sink. As I grasped it, I noticed something was off; the towel was heavier and felt rougher than I expected. Confused, I examined it more closely and found that, while it was the correct size and color, it was of a thicker fabric than I was used to. My roommate, new to the apartment at the time, had brought linen tea towels and put one in our shared kitchen. Knowing exactly how my cotton towels should feel from years of everyday use, these minor changes in weight and texture gave me pause. Yet I could still lift the tea towel with ease, my grip adjusting automatically and my arm moving smoothly as I proceeded to dry the dishes.

This example highlights the complex relationship of somatosensory information and movement and the role that predictions play in allowing us to interact seamlessly with our environment. When handling a familiar object, we plan our movements using implicit expectations about their sensory consequences, allowing predictable sensations to fade into the background of our experience. Sensory signals stand out to us when they diverge from what we predict or become relevant to successfully perform the movement. In this way, predictions do not broadly suppress sensory signals, but regulate how strongly tactile information contributes to perception and movement depending on current demands.

What is driving these changes in tactile perception during movements? This thesis will examine how sensorimotor predictions influence the perception of touch and how tactile processing dynamically changes over the course of a goal-directed movement. It will also include a closer look at the neural correlates of naturalistic vibrations, which will inform our understanding of where in the processing stream tactile perception is modulated according to the behavioral relevance of tactile signals during movements.

1.1 Tactile suppression

The opening example hints at how tactile sensations associated with movement typically do not dominate our perceptual experience. Indeed, tactile sensitivity on a moving limb is lower than at rest (Chapman et al., 1987). This phenomenon known as *tactile suppression* can be measured using psychophysical paradigms such as detection or discrimination tasks, in which an external stimulation on the moving limb is applied to probe perceptual changes in tactile sensitivity associated with movements. Using the same paradigm of externally applied stimulation, tactile processing can be examined by recording somatosensory evoked potentials (SEPs), typically elicited by

electrical stimuli, at different stages of the somatosensory pathway. The reduction in neural responses to tactile stimuli in the context of movements is referred to as *tactile gating*. Although these two terms are sometimes used inconsistently in the literature (e.g., Kilteni & Ehrsson, 2022), suppression is used here to describe perceptual effects and gating to describe neural effects.

Movement-related sensory suppression is not unique to the tactile domain but reflects a broader phenomenon observed also in the vestibular (Cullen, 2019) and auditory modalities (Schröger et al., 2015). Moreover, downregulation of movement-related sensory gain has been demonstrated across the animal kingdom, including in mammals such as primates (Chapman et al., 1988), rodents (Chakrabarti & Schwarz, 2018; Schneider et al., 2014), and domestic cats (Ghez & Pisa, 1972) as well as in fish (Bell, 1981; Wallach & Sawtell, 2023) and invertebrates (Poulet & Hedwig, 2002), underscoring that this mechanism is fundamental to sensorimotor processing.

Tactile suppression and gating generalize across a variety of movements ranging from simple finger abduction (Lei et al., 2018; Williams & Chapman, 2002) or elbow movement (Chapman et al., 1988; Chapman & Beauchamp, 2006) to multi-joint movements like walking (Duysens et al., 1990; Mouchnino et al., 2015), and goal-directed reaching and grasping (Colino et al., 2014; Horn et al., 1996). They have also been reported during isometric contractions demonstrating that motor activity is a key factor as opposed to movement through space (Jiang et al., 1990; Williams & Chapman, 2002). In oscillatory, single-joint movements such as finger abduction, tactile suppression and gating begin shortly before movement onset, with electromyographic recordings showing that this sensory modulation precedes detectable motor activity (Starr & Cohen, 1985; Williams et al., 1998). This anticipatory effect has been attributed to efference copies, which form the basis for downregulating tactile sensitivity and neural responses already during motor planning (Chapman & Tremblay, 2016).

1.2 Sensorimotor predictions and forward models

When planning a movement, the brain creates efference copies of motor commands (von Holst & Mittelstaedt, 1950). An internal forward model uses the current state of the motor system and these efference copies to predict the sensory consequences of the upcoming movement (Miall et al., 1993). Such sensorimotor predictions have several advantages. First, they enable faster and more accurate motor control than relying on delayed and noisy sensory feedback (Miall & Wolpert, 1996). Second, they help filter afferent feedback generated during the movement by suppressing predictable sensations. While some sensory feedback is useful, for example in supporting

online motor control under uncertainty or in processing novel input (Wolpert & Flanagan, 2001), other signals may be redundant or disruptive (Azim & Seki, 2019; McComas, 2016). The internal model is updated by comparing predicted sensory consequences with actual sensory feedback (Wolpert & Ghahramani, 2000). This comparative mechanism is essential not only for updating predictions, but also for distinguishing between reafferent signals, generated by the individual's own movement, and afferent signals caused by external sources (Miall & Wolpert, 1996). Dysfunction in this mechanism has been implicated in clinical conditions such as schizophrenia (Frith et al., 2000) and obsessive-compulsive disorder (Belayachi & Van der Linden, 2010). In sum, sensorimotor predictions enable motor control, filter incoming signals and contribute to distinguishing between self-generated and externally generated sensory events.

The importance of sensorimotor predictions is underscored by findings of tactile suppression even in the absence of actual movement. For instance, tactile suppression has been reported in the planning phase of a movement, even when the subsequent movement execution is prevented by transcranial magnetic stimulation over the motor cortex (Voss et al., 2006). Interestingly, however, tactile suppression and gating have also been observed during passive limb movements (Chapman & Beauchamp, 2006; Huttunen & Hömberg, 1991). Such movements generate somatosensory signals through changes in muscle length, joint position, tendon tension, and skin stretch, but occur in the absence of efference copies. Thus, afferent inflow alone can elicit tactile gating and suppression, suggesting that both efference copy signals and afferent feedback independently shape tactile processing. Moreover, even during passive movements, tactile suppression has been reported for stimuli presented prior to movement onset, suggesting that afferent signals generated by the movement may interfere with processing earlier tactile input, a phenomenon called *backward masking* (Williams & Chapman, 2002). Crucially, however, suppression is stronger and begins earlier during active compared to passive movements (Arikan et al., 2024; Chapman & Beauchamp, 2006), reinforcing the idea that predictive mechanisms play a key role in tactile suppression, alongside afferent processes.

Nevertheless, the role of sensorimotor predictions in tactile suppression has been questioned (Kilteni & Ehrsson, 2022; Press et al., 2020). Tactile suppression is typically measured using externally applied stimuli to probe tactile sensitivity. These tactile probes are not predicted on the basis of an efference copy, as they are not expected sensory consequences of the planned movement. Therefore, it has been argued that the reduction in sensitivity observed in these paradigms may reflect a

general cancellation of somatosensory signals, rather than the specific suppression of predicted sensory events as proposed by forward model accounts (Kilteni & Ehrsson, 2022; Press et al., 2020). Although previous studies underscore the role of central predictive mechanisms, for example by demonstrating the prospective nature of suppression even in the absence of movement (Voss et al., 2006), they have not directly tested whether suppression is driven by *specific* sensorimotor predictions. In Study 1, this question was addressed by manipulating the match between externally applied probes and the predicted sensory consequences of the movement to test whether this alters the magnitude of tactile suppression.

1.3 Context-dependent modulation of tactile suppression and gating

The extent to which tactile processing is reduced during movements is not fixed, but modulated by movement parameters and demands of the motor task. For instance, faster movements have been shown to increase tactile suppression (Angel & Malenka, 1982; Cybulska-Klosowicz et al., 2011) and gating (Rauch et al., 1985; Rushton et al., 1981). Similarly, higher electromyographic (EMG) activity is associated with stronger gating (Sugawara et al., 2016). These findings suggest that increased afferent inflow, due to faster or more forceful movements, may enhance gating and suppression, possibly via masking of incoming tactile signals by concurrent movement-related afferent signals.

However, tactile suppression is not solely determined by the strength of afferent signals. In a somatosensory-guided reaching task, tactile suppression was present throughout the movement but disappeared around the time of maximum speed (Voudouris & Fiehler, 2021). This phase marks the transition into the deceleration phase of the movement, when the hand must be guided accurately towards the target (Elliott et al., 2001). The release from suppression occurred despite ongoing motor activity and high movement speed, suggesting that tactile sensitivity was preserved to meet increased somatosensory feedback demands. These findings point to a dynamic regulation of tactile suppression according to the task relevance of sensory feedback, potentially reflecting a shift from feedforward towards feedback-driven control during critical movement phases (Gallivan et al., 2016; Wolpert & Flanagan, 2001). Additional evidence for the preservation of task-relevant tactile feedback comes from reach-to-grasp movements, where suppression is lower on the index finger used for precision grip compared to other areas of the arm and hand (Colino et al., 2014; Manzone et al., 2018). Similarly, during object manipulation, tactile suppression is reduced when grasping an unseen slippery object compared to a high-friction one (Voudouris &

Fiehler, 2022), and when lifting an object with an unpredictable versus predictable weight distribution in a stable manner (Voudouris et al., 2019). This flexible modulation in tactile suppression also extends beyond fine motor control, with tactile sensitivity on the leg recovering shortly before a balance perturbation, possibly in preparation for compensatory postural adjustments (Wachsmann et al., 2025b). While these findings demonstrate a context-dependent regulation of suppression at the behavioral level, it remains unclear how this modulation is reflected in neural processing.

There is initial evidence that early cortical responses, reflecting preconscious processing (Forschack et al., 2020; Schröder et al., 2021), may be preserved for task-relevant sensations. For instance, short-latency SEPs following sural nerve stimulation in the lower limb are larger during a balancing task when perturbations are expected, which may reflect the preservation of somatosensory signals for posture control (McIlroy et al., 2003). Similarly, Knecht et al. (1993) reported greater amplitude of the short-latency N28 elicited by median nerve stimulation when the stimulated hand actively explored objects, compared to rest, passive tactile stimulation at rest, or active and passive finger flexion and extension. Likewise, the early magnetoencephalographic component M38 to median nerve stimulation was enhanced during skilled object manipulation compared to movements with lower precision demands (Wasaka et al., 2017, 2021).

These findings suggest that temporal modulations of tactile suppression according to task relevance may involve mechanisms in early somatosensory processing. However, since behavioral and neural measures have largely been studied separately, the link between context-dependent modulations in tactile suppression and cortical gating remains unclear. In Study 3, I investigated whether early cortical responses are sensitive to feedback demands, and whether these neural modulations align with dynamic changes in tactile suppression. To do this, psychophysics were combined with electroencephalography (EEG) during a somatosensory-guided reaching task, where tactile suppression has been previously shown to vary across critical movement phases (Voudouris & Fiehler, 2021). To replicate this behavioral effect and avoid introducing additional sources of variation, I adhered closely to the vibrotactile stimulation paradigm used by Voudouris and Fiehler (2021), rather than switching to electrical nerve stimulation. As gating is predominantly reflected in short-latency SEPs occurring within the first ~50 ms after stimulus onset, Study 3 focused on these early responses. Because such short-latency responses are well established for electrical nerve stimulation but remain insufficiently characterized for vibrotactile stimulation, Study 2 first addressed this gap.

1.4 Measurement of early somatosensory processing

SEPs provide a temporally precise measure of somatosensory processing and are therefore well suited to examine the timing of neural modulations during movement. Tactile gating has been reported predominantly for early stimulus encoding reflected in short-latency components including the subcortical P14 (Desmedt & Cheron, 1982; Lei et al., 2018), the cortical N20 (Rossini et al., 1996; Rushton et al., 1981; Tsuji et al., 1984) and the cortical P45 (Allison et al., 1992; Cohen & Starr, 1987; Rushton et al., 1981). Accordingly, assessing modulations of gating requires reliable measurements of short-latency SEPs.

Traditionally, these components are evoked using transcutaneous electrical stimulation of the median or ulnar nerve at the wrist or thumb, which carry somatosensory afferents. Although widely used to investigate signal transmission along the somatosensory pathway and to assess its integrity for diagnostic purposes (Cruccu et al., 2008; Giblin, 1964), this approach is physiologically non-naturalistic. Natural touch is encoded through the activation of cutaneous mechanoreceptors that are tuned to distinct stimulus features and are recruited in characteristic combinations (Bolanowski et al., 1988). In the glabrous skin, low-frequency vibrations are encoded by Meissner corpuscles and rapidly adapting type I fibers (RAI), high-frequency vibrations excite Pacinian corpuscles and RAI fibers, while static skin indentation engages Merkel's discs and slowly adapting type I (SAI) fibers and skin stretch is encoded by Ruffini endings and SAI fibers (McGlone & Reilly, 2010). In contrast, transcutaneous nerve stimulation directly activates heterogeneous fiber populations with spatially distributed receptive fields, including cutaneous and proprioceptive afferents, motor efferents, and smaller-diameter nociceptive fibers (Cruccu et al., 2008). Moreover, the temporal pattern of this activation is highly synchronized with single impulses occurring simultaneously as opposed to the distributed, repetitive firing from natural touch (Gardner et al., 1984). Further, stimulation intensity is constrained by motor and pain thresholds (Andersen et al., 1994; Cruccu et al., 2008). Even within this restricted intensity range, electrical stimulation can be unpleasant to participants, particularly for populations like patients, children or older adults.

Vibrotactile stimulation elicits a more naturalistic activation pattern and the stimulation parameters can be tailored to selectively target specific mechanoreceptors and cutaneous afferent subtypes. Despite this advantage, vibrotactile stimulation remains comparatively underused in SEP paradigms. Notably, many vibration studies fail to observe short-latency components reflecting processing at thalamocortical and early

cortical stages (Hämäläinen et al., 1990), focusing instead on later SEPs such as the P100, N140, P200, and P300 (Juravle et al., 2016; Morozova et al., 2024; Park et al., 2021). These components are linked to higher-order processing including stimulus detection, evaluation and report (Schröder et al., 2021). One explanation for the absence of early components is the reduced temporal and spatial synchrony of peripheral afferent activation compared with electrical stimulation. Alternatively, because short-latency SEPs are small in amplitude relative to later components, their absence may reflect methodological constraints rather than physiological differences. These include low stimulation intensities, limited sampling rates, low trial numbers or small sample sizes (Choi et al., 2020; Hämäläinen et al., 1990), all of which reduce signal-to-noise ratios. Moreover, vibratory SEPs remain less well characterized overall. For example, the influence of vibration intensity has been documented for late components such as the P200 and P300 (Park et al., 2021), but not for earlier SEPs.

Study 2 addressed this gap in the literature and provides a comprehensive overview of SEPs for naturalistic vibrations in the preferred range of Pacini corpuscles. Specifically, Study 2 examines the effects of stimulation amplitude on SEPs and compares the waveforms and source activations from vibrotactile stimulation with those elicited by electrical stimulation. By detailing short-latency SEPs following vibration, Study 2 also establishes the methodological basis for the joint investigation of tactile suppression and early cortical gating in Study 3.

1.5 Research objectives

This thesis examines the predictive and context-dependent nature of tactile suppression, as well as the neural correlates of naturalistic vibrations. Study 1 investigates whether suppression is selectively modulated by precise predictions or reflects a general reduction in tactile sensitivity independent of sensorimotor predictions. Feedforward models propose that internal models predict the sensory consequences of an action and suppress predictable sensations, yet it remains unclear whether suppression of externally applied probes is specifically tuned to expected sensory consequences. Using a paradigm that established predictable sensory consequences of a movement, tactile sensitivity was assessed for external vibrotactile probes that either matched or deviated from these predicted consequences. Study 2 addresses a gap in the SEP literature, which predominantly relied on electrical stimulation, by characterizing SEPs elicited by naturalistic vibrotactile stimulation targeting Pacinian mechanoreceptors and RAI afferents. This study provides an overview of vibrotactile SEPs, examines their scaling with stimulation amplitude, and compares their

waveforms and source activations with those evoked by electrical stimulation. Study 3 builds on the vibrotactile stimulation protocol established in Study 2 to examine whether context-dependent modulations of tactile suppression during goal-directed reaching are reflected in early cortical processing. Using a combined approach of psychophysics, EEG and kinematics, Study 3 tests whether changes in tactile sensitivity across critical movement phases are accompanied by corresponding modulations of the short-latency P45 component. Together, these studies outline the role of sensorimotor predictions in tactile suppression, characterize the SEPs elicited by naturalistic vibrations, and use this approach to investigate the neural correlates of context-dependent modulation of tactile suppression.

2 Study I: Tactile suppression stems from specific sensorimotor predictions

Fuehrer, Voudouris, Lezkan, Drawing & Fiehler, 2022, Proceedings of the National Academy of Sciences of the United States of America

The first study investigated whether tactile suppression reflects specific sensorimotor predictions. Participants used their right index finger to stroke across objects with either a coarse or a fine texture, eliciting low- or high-frequency vibrations on the fingertip, respectively (Figure 1A). The frequencies were selected to fall within ranges preferentially activating Meissner/RAI afferents at low frequencies and Pacinian/RAII afferents at high frequencies, biasing the stimulation toward different cutaneous afferent subtypes (Bolanowski et al., 1988). The textured objects were presented in blocks to enable clear sensorimotor predictions of the vibration frequencies caused by stroking across the objects at a set speed that participants practiced prior to the experiment. Before movement onset, weak vibrotactile stimulations of varying amplitudes were delivered to the right index finger to probe tactile sensitivity (Figure 1B). These probes were either congruent or incongruent with the frequency elicited by the objects (Figure 1C). To isolate movement-related suppression, participants also performed the detection task at rest.

Tactile sensitivity was significantly lower for probes congruent with the predicted frequency than for incongruent probes (Figure 1D), indicating that suppression was specifically tuned to predicted sensory consequences. This congruency effect could not be explained by response bias or movement kinematics. Interestingly, the congruency effect occurred alongside a general reduction in sensitivity for both types of probes relative to rest. This suggests sensorimotor predictions broadly downregulate

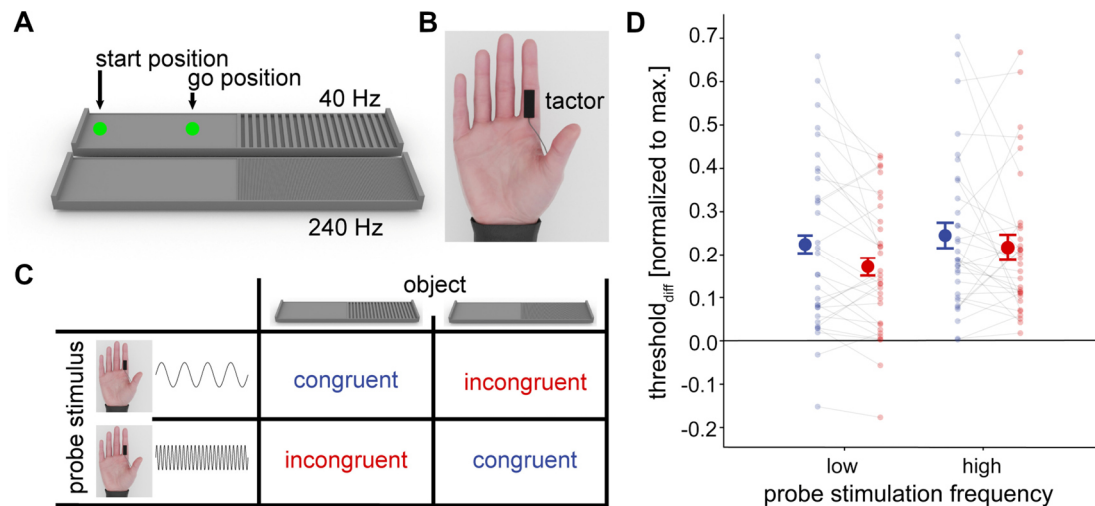


Figure 1. Experimental paradigm and tactile suppression.

A. Participants first moved along the smooth part of the object from the start position to the go position at their own pace to avoid adaptation to the texture. From there, they stroked across the remaining object surface at a speed chosen to elicit a vibration of 40 Hz and 240 Hz for the coarse and fine texture respectively. B. Just before movement onset, a tactor delivered probe stimulations to the palmar side of the right index finger. C. Probe stimulations either matched (congruent) or deviated (incongruent) from the frequency elicited by stroking across the texture. D. Tactile sensitivity was reduced compared to rest, with stronger suppression for congruent probes, demonstrating a precise predictive tuning of tactile. Error bars represent 95% Cousineau-Morey confidence intervals for the congruency effect at each probe stimulation frequency.

somatosensory processing during movement planning, while predicted sensory consequences are subject to additional, stimulus-specific suppression.

3 Study II: Characterizing SEPs from Pacinian-targeted vibrations

Fuehrer, Maurer & Fiehler, 2025, Journal of Neurophysiology

The second study examined short-latency SEPs elicited by high-frequency vibrations targeting Pacini corpuscles to establish a reliable stimulation protocol for assessing neural responses to naturalistic tactile stimuli. The study characterized SEP waveforms evoked by vibrotactile stimulation, examined their scaling with vibration amplitude, and compared them to SEPs from cutaneous electrical stimulation. Participants rested their hands on a table while sinusoidal vibrations (20 ms, 280 Hz) of four suprathereshold intensities were presented on the index finger (Figure 1B) in random order with an interstimulus interval of 2200 ms. In a subset of participants, this protocol was repeated in a different session using electrical stimulation at the same site, with intensities selected in a pilot study to match the vibrotactile stimuli in perceived intensity. In the main experiment, the two lower and two higher electrical intensities were

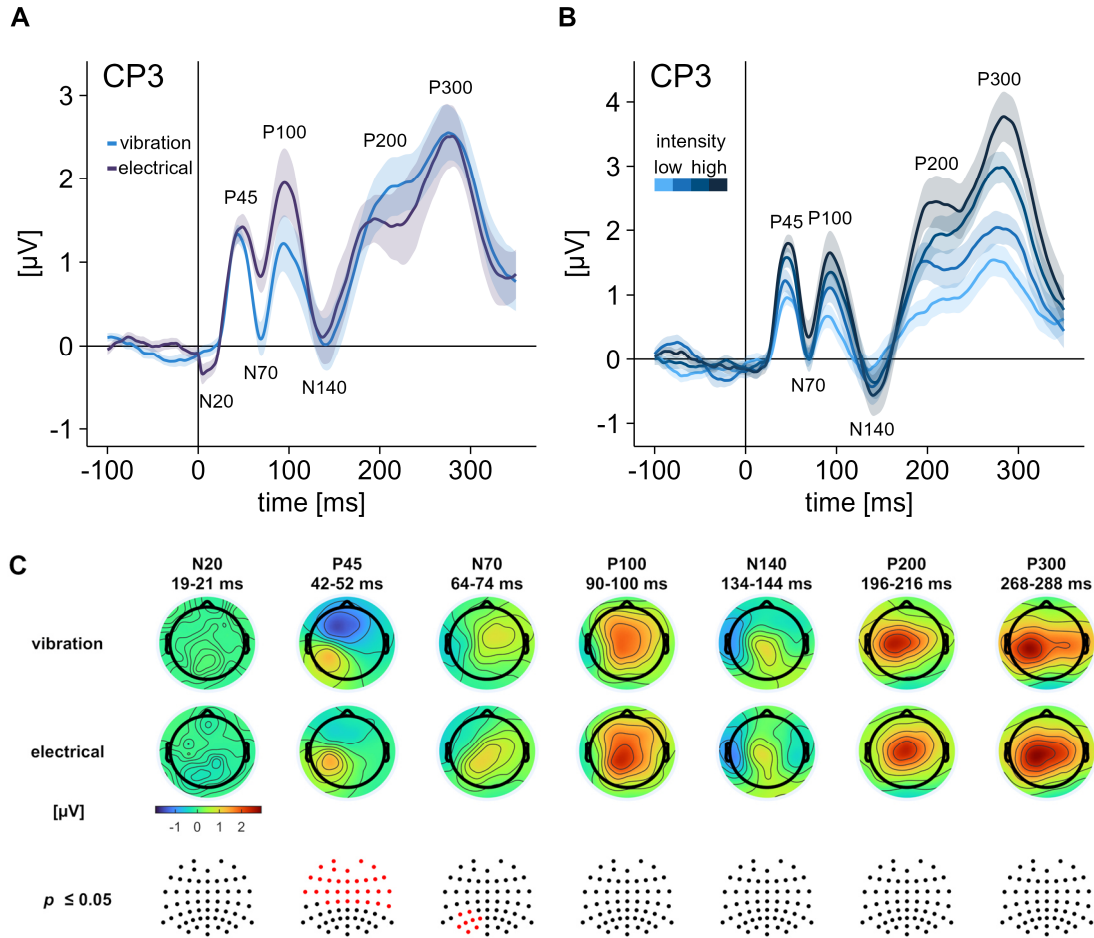


Figure 2. EEG responses to electrical and vibrotactile stimulation.

A. Grand-average EEG waveforms at electrode CP3 contralateral to electrical and vibrotactile stimulations showing an N20 for electrical stimulation and a P45, N70, P100, P200 and P300 for both modalities. B. Grand-average EEG waveforms following vibrotactile stimulation of four different suprathreshold amplitudes. The amplitude of the P45, P100, P200 and P300 increased with vibration intensity while the N140 decreased. C. Topographies differed between stimulation modalities during the time windows of the P45 and N70. Vibrotactile stimulation elicited a stronger fronto-central negativity during the P45 window and greater contralateral centro-parietal activity during the N70. Channels with significant differences are highlighted in red. Shaded area reflects standard error.

presented in separate blocks due to device limitations. Except for the N20, which appeared only after electrical stimulation, both modalities elicited similar SEPs at electrode CP3, contralateral to the stimulated finger, namely, the P45, N70, P100, N140, P200, and P300 (Figure 2A). The amplitudes of the P45, P100, P200, and P300 components increased with vibration intensity, and the N140 amplitude decreased (Figure 2B). As a reference for future studies, I further quantified intensity scaling by estimating the change in component amplitude (μV) per increase in vibration amplitude (μm) using linear mixed models.

For electrical stimulation, only the P100 amplitude increased significantly with intensity. However, interpretation of these results was limited because electrical intensities were split up into two separate blocks. This block-wise design also prevented direct comparisons of intensity scaling across stimulation modalities. The topographies of the P45 and N70 differed between vibrations and electrical stimulation (Figure 2C). An exploratory source analysis motivated by these differences revealed stronger activity in contralateral precentral regions and S1 for vibrations in the time window of the P45, while posterior parietal areas and regions around secondary somatosensory cortex (S2) showed distinct activation patterns for the two stimulation modalities. No such differences were observed for the N70. These findings establish naturalistic high-frequency vibrations as a reliable method for measuring SEPs, including the short-latency P45, and demonstrate how they scale with stimulus intensity. They also suggest that early somatosensory processing of RAI-targeted vibrations may differ from the broader activation evoked by electrical stimulation, but converge at later stages.

4 Study III: Temporal dynamics of early somatosensory processing in goal-directed actions

Fuehrer, Voudouris, Maurer & Fiehler, 2026, bioRxiv

In Study 3, the dynamic modulation of tactile suppression and gating during goal-directed reaching was investigated using behavioral and EEG measures. Participants reached with their right hand to one of two target fingers on their left hand using only somatosensory feedback, as both hands were occluded from vision. At one of five possible time points during the reach, a standard vibration of fixed intensity (20 ms, 280 Hz) was presented on the moving right index finger (Figure 1B). A comparison vibration of varying intensity was applied to the sternum after the movement and participants reported which stimulation felt stronger. EEG was recorded to examine the neural responses to tactile stimulation. To isolate SEPs, waveforms from non-stimulation trials at corresponding time points were subtracted from stimulation trials. The task was also performed at rest to account for individual differences in tactile sensitivity. Sensory feedback should be most relevant around maximum speed to guide the hand as the movement transitions from initiation to deceleration (Elliott et al., 2001). Accordingly, stimulations were grouped into four movement phases relative to the time of maximum speed in each trial. Compared with rest, both tactile sensitivity and P45 amplitudes were reduced throughout the movement, but suppression and gating were weaker around maximum speed than near movement end (Figure 3A, B). Notably, no P45 gating was detected around maximum speed. This temporal pattern may reflect

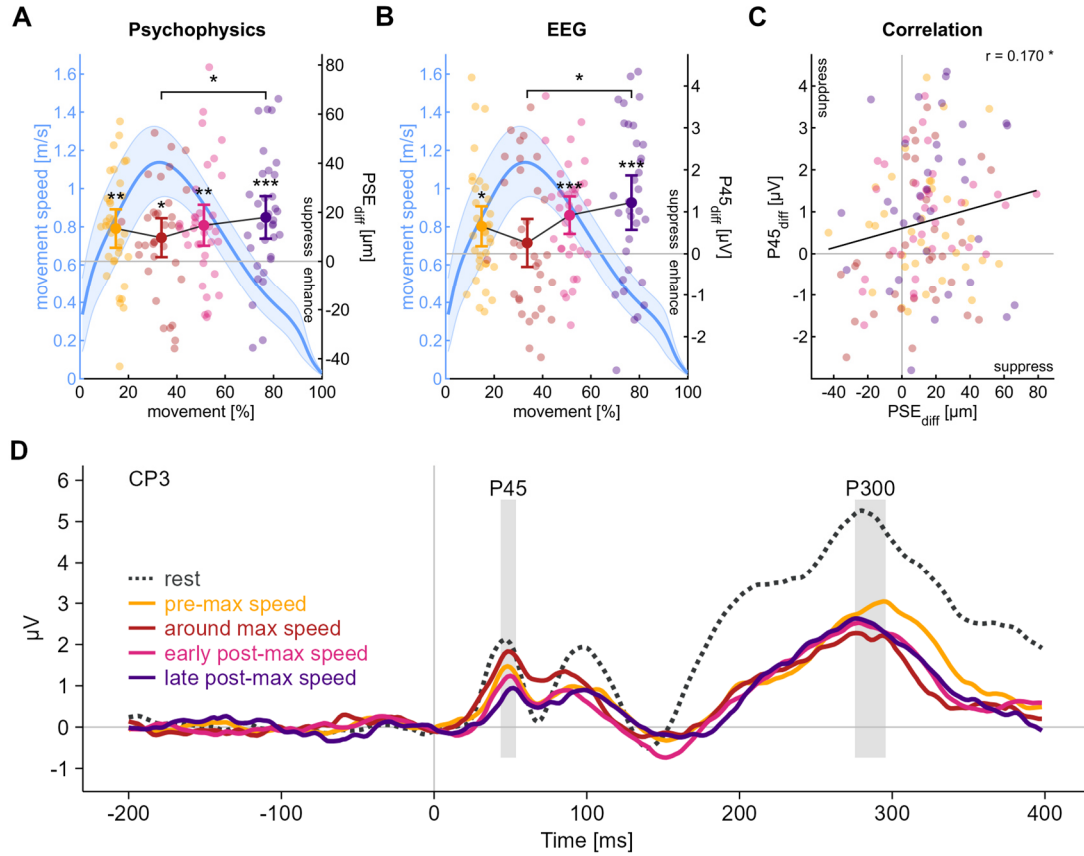


Figure 3. Tactile suppression and gating across movement phases.

A. Mean normalized movement speed over time across participants (blue line, left y-axis; shaded area indicates standard error) and mean tactile suppression relative to rest (PSE_{diff} , right y-axis; error bars reflect 95% confidence intervals) across the four movement phases. B. Mean normalized movement speed over time (blue line) and mean P45 amplitude relative to rest ($P45_{diff}$) across movement phases. C. Scatterplot of $P45_{diff}$ and PSE_{diff} for individual participants across movement phases and pooled ordinary least squares regression of $P45_{diff}$ on PSE_{diff} (black line). Reduced P45 amplitudes correlated with stronger tactile suppression. D. Grand-averaged EEG waveforms following the standard stimulation during the four movement phases and at rest.

heightened feedback demands mid-reach, indicating that both suppression and gating are flexibly regulated in a context-dependent manner. In line with this, stronger tactile suppression correlated with reduced P45 amplitudes, suggesting that changes in tactile sensitivity were linked to early cortical processing (Figure 3C). Meanwhile, the P300, associated with later cognitive processes, showed a uniform reduction throughout the movement (Figure 3D). Together, these findings indicate that the temporal modulation in tactile suppression is more closely related to early than to later stages of somatosensory processing.

5 Discussion

5.1 Predictive mechanisms in tactile suppression

Feedforward models propose that predictions based on efference copies suppress expected sensory consequences of movements (Miall & Wolpert, 1996). Accordingly, stroking one's own hand is perceived as weaker than identical touch from an external source, an effect that disappears when the sensory consequences of self-touch are delayed or spatially distorted (Blakemore et al., 1999). Such paradigms measure the perceived intensity of self-touch where the correspondence between sensorimotor prediction and sensory consequence is intuitive because the participant causes the examined sensation themselves. However, movements generate a broad range of reafferent signals beyond self-touch, such as joint motion, tendon tension, skin stretch, and proprioceptive input, which motor control theories propose are likewise downregulated (Azim & Seki, 2019). To probe tactile sensitivity to these signals during movement planning and execution, external tactile stimuli are commonly applied to the moving limb (Chapman et al., 1987). Because these external probes are not predicted sensory consequences of the movement, it has been questioned whether their suppression reflects specific sensorimotor predictions or a general cancellation mechanism, such as backward masking (Press et al., 2020). Similarly, Kilteni and Ehrsson (2022) propose that the suppression of external probes and of self-touch are independent phenomena, arguing that only the latter can arise from sensorimotor predictions.

Study 1 tested whether sensorimotor predictions contribute to the suppression of external probes by manipulating the match between the predicted sensory consequences of a movement and externally applied vibrotactile stimuli. Probes congruent with the predicted sensory outcome of the movement were suppressed more strongly than incongruent probes, demonstrating that tactile suppression is specifically shaped by sensorimotor predictions. Importantly, the congruency effect could not be explained by differences in kinematic behavior or response bias, indicating a genuine modulation of tactile sensitivity based on the match between the probe and the sensorimotor prediction. While congruent probes were suppressed more strongly than incongruent probes, tactile detection thresholds were elevated relative to rest irrespective of congruency. Backward masking is unlikely to account for this general suppression effect, as probes were presented on average 119 ms before movement onset, which is well outside the ~50-100 ms window reported for tactile backward masking (Abramsky et al., 1971; Fraser & Fiehler, 2018; Kirman, 1984; Williams & Chapman, 2002).

Moreover, all stimulations occurred at least 250 ms before contact with the textured surface, ruling out specific masking from the texture itself. Instead, this general suppression effect likely reflects predictive modulation of somatosensory input based on the anticipated sensory states of the moving arm beyond the vibration generated by contact with the texture. The findings from Study 1 suggest that tactile suppression during movement preparation involves both this broad mechanism and a more specific component tuned to the congruency between the probe and the predicted sensory consequences of touching the textured surface. In sum, Study 1 shows that sensorimotor predictions prospectively modulate tactile sensitivity to external probes during movement preparation and that this modulation is specifically shaped by the predicted sensory consequences of the action.

Beyond sensory consequences, the internal model continuously estimates future system states more generally, such as limb position and velocity (Miall & Wolpert, 1996). These state estimates, together with uncertainty and task demands, implicitly determine how relevant feedback is predicted to be and how strongly it should influence ongoing movements (Franklin & Wolpert, 2011). The transient reduction of tactile suppression and gating observed around maximum speed in Study 3 can therefore be interpreted as a predictively driven upregulation of sensory gain when feedback is anticipated to be behaviorally relevant. In this view, predictive mechanisms specify not only *which* sensory signals are redundant, as shown in Study 1, but also *when* and to *what extent* their processing should be reduced to support feedback-dependent control.

5.2 Context-dependent modulation of tactile suppression and gating

Optimal feedback control formalizes how these predictive state estimates are used to dynamically modulate the influence of sensory feedback according to task demands (Franklin & Wolpert, 2011; Todorov & Jordan, 2002). Consistent with this framework, visuomotor feedback gains in a goal-directed reaching task peak mid-reach, when feedback corrections are still effective, and decline upon approaching the target as control shifts toward stabilization and movement termination (Dimitriou et al., 2013). In the somatosensory-guided reaching task used in Study 3, tactile suppression and gating decreased around maximum speed compared to late in the movement. This relative decrease mid-reach may indicate a brief upregulation in somatosensory gains to guide the hand as the movement enters the deceleration phase (Elliott et al., 2001), while stronger suppression late in the movement may arise from lower precision demands involved in movement termination (Liu & Todorov, 2007). Alternatively, given

the remaining suppression mid-reach, the observed pattern may be driven by increased suppression near movement offset as contact with the target becomes more likely (Fraser & Fiehler, 2018). Critically, tactile gating was absent mid-reach, consistent with a transient upregulation of somatosensory processing followed by a down-regulation towards the movement end in line with optimal feedback control.

Notably, unlike single-joint paradigms where suppression and gating scale with movement speed (Angel & Malenka, 1982; Rushton et al., 1981), sensitivity and early cortical responses peaked at maximum speed, underscoring that tactile processing in complex movements is governed by task demands rather than concurrent afferent inflow. Compared with previous work reporting a complete release from suppression mid-reach using a detection task (Voudouris & Fiehler, 2021), residual suppression in Study 3 likely reflects a higher memory load of the delayed comparison task. In line with this, the P300, which decreases with cognitive load particularly in dual-task situations (Polich, 2007), was gated throughout the movement, whereas the P45, providing an immediate measure of low-level sensory encoding (Schröder et al., 2021), remained intact mid-reach. Hence, maintaining stimulus intensity in working memory during the movement may have impaired perceptual processing despite intact early sensory encoding. Nevertheless, Study 3 revealed a similar temporal pattern with a transient preservation of tactile sensitivity to support feedback-dependent control. Moreover, EEG results indicate this behavioral pattern may arise, at least partly, from gain control mechanisms during early sensory encoding.

These findings also align with studies on complex lower limbs movements showing transient somatosensory modulations when online feedback is task relevant. For example, tactile sensitivity on a kicking leg increases during the swing phase relative to movement initiation and termination (Wachsmann et al., 2025a). In walking, phase-dependent modulation of the P50-N80 complex has been reported along with indications of similar shifts in tactile sensitivity, suggesting a functional role in monitoring balance and surface characteristics (Altenmüller et al., 1995; Duysens et al., 1990; Mouchnino et al., 2015). Study 3 extends this literature by demonstrating that tactile suppression and gating follow similar distinct temporal dynamics according to feedback demands in upper limb movements. A limitation is that feedback demands were inferred from movement phase. Although the findings were consistent with optimal feedback control, Study 3 did not directly manipulate feedback relevance. Future studies could alter target distance or introduce online target shifts, as in Dimitriou et al. (2013), to test whether the transient reductions in tactile suppression and gating reflect changing feedback demands. Moreover, future studies should combine empirical

measurements of suppression and gating with computational modelling of the movement within an optimal feedback control framework (Liu & Todorov, 2007; Tatai et al., 2026). While Study 3 links behavioral and neural effects via correlation, modelling approaches could test whether the observed changes in tactile sensitivity and early somatosensory responses reflect a common underlying state-estimation process, for example through changes in positional uncertainty across the movement.

5.3 EEG correlates of naturalistic vibrations

While these studies examining context-dependent changes in somatosensory processing have employed electrical stimulation of mixed nerves, Study 3 used high-frequency vibrations targeting RAI fibers specifically. This approach ensured comparability with previous tactile suppression paradigms and made it possible to examine the naturalistic processing of afferent signals. However, vibrations are rarely used in EEG research, and prior work has reported fewer short-latency components for vibrotactile compared to electrical stimulation (Hämäläinen et al., 1990), which posed a challenge for examining tactile gating. To address this gap, Study 2 characterized SEPs elicited by vibrations within the receptive range of Pacinian corpuscles and RAI fibers, establishing a stimulation protocol for future EEG studies.

Centro-parietal SEPs contralateral to vibrotactile stimulation resembled the waveform morphology of cutaneous electrical stimulation from the P45 onwards (N70, P100, N140, P200, P300). Although scalp recordings have limited spatial resolution, the generators of short- and medium-latency somatosensory SEPs have been validated via intracranial recordings in humans and non-human primates (Allison et al., 1992; Arezzo et al., 1981). The P45 originates primarily from areas 3b and 1 of contralateral S1 (Allison et al., 1992; Buchner et al., 1994; Hämäläinen et al., 1990) with possible contributions from S2 (Karhu & Tesche, 1999). The N70 reflects processing in contralateral S1 and S2, whereas the P100 arises from bilateral S2 (Allison et al., 1992; Jung et al., 2009). The N140 has bilateral contributions from frontal regions and the supplementary motor area (Allison et al., 1992) and marks the earliest correlate of tactile awareness (Schröder et al., 2021). The P200 and P300 reflect higher-order processing, including evaluation and reporting of tactile input (Schröder et al., 2021).

The earlier N20 component, generated in area 3b of primary somatosensory cortex in response to thalamocortical input (Allison, 1982; Tsuji et al., 1984) was observed only following electrical stimulation. This was despite a larger sample size, higher sampling rate, more trial repetitions than used previously, and matched stimulation intensity across modalities (Choi et al., 2020; Hämäläinen et al., 1990). Therefore, the

absence of components prior to 45 ms for vibrations may indeed reflect the lower synchrony of mixed sensory fiber activation achieved by electrical stimulation, although the N20 has previously been reported for air puffs (Kawohl et al., 2007; Rossini et al., 1996).

Study 2 replicated previous findings of amplitude-related modulation of the P200 and P300 for vibrotactile stimulation (Park et al., 2021), and extends them by demonstrating similar scaling of the P45, P100 and N140, which has previously been reported for electrical stimulation (Brennum & Jensen, 1992; Schröder et al., 2021). No comparable modulation of the N70 was observed, despite previous reports using air puffs (Hashimoto et al., 1988), likely due to limited statistical power.

Topographical comparisons between the two stimulation modalities revealed differences during the P45 and N70 time windows. An exploratory source analysis motivated by these differences showed stronger contralateral activation for vibrations in precentral and S1 regions, with distinct activation in posterior parietal areas and S2 subregions for early processing (P45) but no differences between stimulation modalities at a later stage (N70). Previous studies have reported stronger S1 activation for electrical compared to mechanical stimulation, but have not accounted for intensity differences between modalities, likely inflating the effect of electrical stimulation (Forss et al., 1994; Rossini et al., 1996; but see Alouit et al., 2025). Because perceived intensities were matched in Study 3, the observed differences likely reflect receptor-specific processing rather than stimulus strength. As both modalities were applied to the index finger, electrical stimulation presumably activated cutaneous fibers with minimal motor fiber involvement (Rigoard, 2020), indicating that differences arose from broad, synchronized versus selective cutaneous fiber activation. The relatively low stimulation intensities suggest that any contribution from small-diameter nociceptive afferents was likely minimal (Cruccu et al., 2008). Overall, these findings suggest that early cortical responses may differ between naturalistic and electrical stimulation, while later processing converges. As these findings stem from exploratory source analyses without individual head models, inferences regarding specific cortical generators remain tentative. The observed modality-dependent differences can guide future hypothesis-driven studies using methods with higher spatial precision.

5.4 Neurophysiological mechanisms of predictive and context-dependent gain control

Study 1 showed that tactile suppression arises from specific predictions that down-regulate expected and therefore redundant sensory input. Study 3 extended this by

demonstrating that suppression and gating are dynamically modulated by task relevance. Together, these findings suggest that tactile suppression and gating reflect predictive gain control sensitive to motor context. But how is this flexible sensory tuning implemented neurophysiologically? Neural responses in Study 3 indicate that this modulation is expressed at early stages of S1 processing. The ascending somatosensory pathway offers several opportunities to regulate afferent inflow before reaching S1. First-order neurons from low-threshold mechanoreceptors enter the spinal cord via the dorsal root and ascend to the dorsal column nuclei in the brainstem (Abraira & Ginty, 2013), where they form the first synapse and a first site for tactile gating (Ghez & Pisa, 1972). Second-order neurons project via the medial lemniscus to the thalamus, and third-order neurons target S1 (Abraira & Ginty, 2013), with evidence of tactile gating at each level (Chapman et al., 1988).

Spinal gating is mediated by interneuron circuits that reduce transmission of sensory afferents via presynaptic inhibition (Bui et al., 2015). Notably, this early spinal gain control can be highly specific. Confais et al. (2017) show that cutaneous input is suppressed during wrist movement, whereas proprioceptive input from wrist extensor muscles is selectively facilitated during extension but not flexion. Importantly, this input-specific and task-dependent modulation emerges during an instructed delay period prior to movement, consistent with central anticipatory control (Confais et al., 2017). Selective inhibition has also been reported between group Ia and Ib proprioceptive afferents (Rudomín et al., 1983). By analogy, the frequency-specific suppression observed in Study 1 may reflect similar inhibitory tuning between cutaneous RAI and RAI afferents, although direct evidence for this is lacking. Critically, presynaptic inhibition is at least in part under descending control from the brainstem and cortex and precedes EMG activity in voluntary movements in primates, consistent with a centrally generated predictive mechanism (Seki et al., 2003). In line with cortical control of subcortical gating, lesioning descending projections from S1, S2, and posterior parietal cortex abolishes gating at the first synapse in rodents (Chakrabarti & Schwarz, 2018). In humans, S1 and S2 along with supplementary motor cortex are also involved in tactile suppression (Arikan et al., 2021; Haggard & Whitford, 2004).

Stronger gating at cortical than subcortical levels points to additional intracortical mechanisms for gain control (Lei et al., 2018; Seki & Fetz, 2012). For example, signals from motor areas can activate local inhibitory circuits within the sensory cortex. In rodents, a substantial proportion of auditory gating is generated locally within auditory cortex, where excitatory inputs from motor cortex recruit inhibitory interneurons (Schneider et al., 2014). By a similar mechanism, frequency-specific gating of

reafferent sounds has been demonstrated in rodent auditory cortex (Schneider et al., 2018). Given this neurophysiological architecture, predictive mechanisms could plausibly regulate both afferent inflow into the cortex and intracortical inhibition to specifically suppress redundant sensations and regulate somatosensory processing according to motor context. Notably, the absence of temporal tuning in the later P300 component in Study 3 argues against a late cognitive origin and instead implicates early sensorimotor mechanisms. Clarifying the contribution of subcortical and cortical stages in the predictive and context-sensitive modulation of sensory gain will require future studies probing gating at multiple levels of the somatosensory pathway alongside psychophysics.

Functionally, such flexible tuning is critical because sensorimotor control is bidirectional. Sensory afferents regulate motoneuron excitability via spinal interneurons, enabling cutaneous and proprioceptive inputs to shape reflexes and adjust motor output during movement (Bui et al., 2015; Panek et al., 2014). Removing presynaptic inhibition of proprioceptive afferents introduces tremors during reaching, consistent with excessive feedback gains (Fink et al., 2014), while eliminating cutaneous feedback via local anesthesia increases hand path variability (Gentilucci et al., 1997), demonstrating that motor control relies on balanced somatosensory feedback. This balance is maintained by descending corticospinal projections which modulate spinal sensorimotor integration and exert top-down control over sensory influences on motor output (McComas, 2016; Ueno et al., 2018). In sum, tactile suppression and its modulation are likely the behavioral expression of distributed predictive gain-control regulating somatosensory feedback during movement planning and execution (Azim & Seki, 2019).

5.5 Future directions

A key question for future work is the relationship between the suppression of external probes and self-touch. Existing evidence leaves open whether the two forms of suppression are independent, as proposed by Kilteni and Ehrsson (2022), or whether self-touch attenuation is a more strongly constrained instance of a broader sensory gain-control mechanism that can also be assessed through external probes (Kilteni et al., 2025). Since sensorimotor predictions clearly shape both self-touch attenuation (Blakemore et al., 1999) and the suppression of external probes (Study 1), apparent discrepancies may reflect paradigm differences in parameters such as stimulus predictability, rather than independent mechanisms (Kilteni & Ehrsson, 2022). Consequently, future studies may gain more by characterizing their paradigms along a set

of key parameters, rather than contrasting self-touch attenuation and suppression of external probes as separate phenomena. In addition to the source of the sensory event, these parameters include the predictability of the examined sensation based on the motor command across space, time, and feature congruency (e.g. vibration frequency). They also include the state of the tested limb, that is, whether perception is assessed on a moving or resting limb, and the movement phase at the time of measurement. Finally, they include the behavioral relevance of sensory feedback on the examined limb, that is, whether it supports online motor control, informs about a successful outcome at the movement endpoint, or is irrelevant for motor control.

Framing the problem in this more nuanced way would allow existing evidence to be evaluated in terms of these parameters and would guide future studies to test movement-related suppression within unified designs that systematically quantify their effects. This could also inform critical questions about the anatomical site and stage at which each parameter modulates somatosensory processing, including the relative contributions of subcortical and cortical circuits. Ultimately, establishing a parameter-driven framework for movement-related sensory suppression would provide common ground for assessing whether similar principles govern sensory suppression in other modalities, such as audition (Schröger et al., 2015), and for interpreting contrasting findings in the visual domain (Press et al., 2020; Schwarz et al., 2018).

6 Conclusion

This thesis has shown that tactile perception in the context of movement is shaped by precise sensorimotor predictions and the behavioral relevance of sensory feedback. Returning to the act of picking up a familiar towel, somatosensory processing on the reaching hand was likely tuned across movement phases according to feedback demands. Before grasping the towel, its weight and texture were predicted based on previous interactions. These predictions suppressed redundant sensations, whereas the changes in weight and texture stood out and increased the influence of sensory feedback in guiding the hand while drying the dishes. At the neural level, this process was likely reflected in early stages of processing. The studies presented here suggest that, rather than a general reduction in somatosensory processing, tactile suppression represents a precise, predictive gain-control mechanism that tunes sensory feedback to current motor demands, enabling smooth, adaptive interactions with the environment.

7 References

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II Publications

1 List of publications

Fuehrer, E., Voudouris, D., Lezkan, A., Drewing, K., & Fiehler, K. (2022). Tactile suppression stems from specific sensorimotor predictions. *Proceedings of the National Academy of Sciences*, 119(20), e2118445119. <https://doi.org/10.1073/pnas.2118445119>

Fuehrer, E., Maurer, L. K., & Fiehler, K. (2025). Characterizing SEPs from Pacinian-targeted vibrations. *Journal of Neurophysiology*, 134(4), 1185–1196. <https://doi.org/10.1152/jn.00304.2025>

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2 Study I: Tactile suppression stems from specific sensorimotor predictions



Tactile suppression stems from specific sensorimotor predictions

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The ability to sample sensory information with our hands is crucial for smooth and efficient interactions with the world. Despite this important role of touch, tactile sensations on a moving hand are perceived weaker than when presented on the same but stationary hand. This phenomenon of tactile suppression has been explained by predictive mechanisms, such as internal forward models, that estimate future sensory states of the body on the basis of the motor command and suppress the associated predicted sensory feedback. The origins of tactile suppression have sparked a lot of debate, with contemporary accounts claiming that suppression is independent of sensorimotor predictions and is instead due to an unspecific mechanism. Here, we target this debate and provide evidence for specific tactile suppression due to precise sensorimotor predictions. Participants stroked with their finger over textured objects that caused predictable vibrotactile feedback signals on that finger. Shortly before touching the texture, we probed tactile suppression by applying external vibrotactile probes on the moving finger that either matched or mismatched the frequency generated by the stroking movement along the texture. We found stronger suppression of the probes that matched the predicted sensory feedback. These results show that tactile suppression is specifically tuned to the predicted sensory states of a movement.

sensorimotor prediction | efference copy | tactile suppression | sensory gating | tactile attenuation

Tactile sensations on a moving limb are suppressed compared to rest (1, 2). Movement-induced suppression is a fundamental phenomenon of sensory processing found at both the neural and the perceptual level (3) and across various mammalian species, such as human and nonhuman primates (1, 4), cats (5), and rats (6–8). Tactile suppression, sometimes also called tactile gating (9), is commonly tested by applying externally generated tactile probes on a limb that is moving; a well-established paradigm that allows quantifying tactile suppression at various body parts and times (10–12). Tactile suppression is modulated by different spatial and temporal factors. It is most pronounced when the tactile probe is in close proximity to the muscles involved in the movement and gradually decreases when the probe is at more distant locations (13). It can precede the onset of muscle activity and persist throughout the movement (10, 13). Moreover, it can be modulated by task-relevancy, such that suppression is reduced or even eliminated entirely as the importance of sensory feedback increases (11, 14–16).

There is strong evidence that tactile suppression on a limb depends on a forward model. This model uses online feedback and an efference copy of the motor command to estimate the limb's future sensory states and suppress the predicted sensory feedback (17). Indeed, suppression occurs during the planning phase of a movement (i.e., in the absence of movement) (12) and is stronger with more reliable predictions about the prevailing dynamics (16). Neural effects in central somatosensory and motor areas before movement (18, 19) further corroborate the involvement of central, predictive mechanisms. Yet, reports of tactile suppression shortly before and during passive movements indicate that peripheral, reafferent signals may also mask the detection of tactile probes (20), although suppression before active movements may precede the effects observed in passive movements (4, 21). The possibility of backward masking mechanisms as well as the fact that the external tactile probes cannot be predicted by an efference copy of the motor command have led to recent claims that the reduced sensitivity on a moving limb is rather caused by general cancellation policies, and tactile suppression of externally generated stimuli is independent of sensorimotor predictions (22, 23). Here, we aim to resolve this debate by investigating whether tactile suppression stems from such precise sensorimotor predictions or whether it originates from an unspecific mechanism that leads to a blanket reduction in tactile sensitivity and thus does not distinguish between predicted and unpredicted sensory feedback.

Significance

Tactile sensations on a moving hand are perceived weaker than when presented on the same but stationary hand. There is an ongoing debate about whether this weaker perception is based on sensorimotor predictions or is due to a blanket reduction in sensitivity. Here, we show greater suppression of sensations matching predicted sensory feedback. This reinforces the idea of precise estimations of future body sensory states suppressing the predicted sensory feedback. Our results shine light on the mechanisms of human sensorimotor control and are relevant for understanding clinical phenomena related to predictive processes.

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The authors declare no competing interest.

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To determine highly specific suppression effects, we manipulated the congruency between the predicted sensory feedback and the external vibrotactile probes (see Fig. 1 for an overview of the methods). Participants performed single stroking movements along two textured objects at a designated speed. Depending on the spatial frequency of the object's texture, they experienced either a low or a high frequency vibration on their fingertip. These two fundamental frequencies were chosen in a way that different mechanoreceptors were stimulated (24, 25). The objects were presented in a blocked manner so that the tactile feedback from the movement was fully predictable. Vibrotactile probe stimuli were applied to the stroking finger around movement onset. The frequency of these probes either matched (congruent condition) or mismatched (incongruent condition) the frequency elicited on the finger during movement along the textured object. This resulted in four movement conditions: low frequency congruent, low frequency incongruent, high frequency congruent, and high frequency incongruent.

Participants were asked to respond whether they detected the probe stimulus in each trial. We fitted psychometric functions to the individual responses and first calculated the difference in tactile detection thresholds ($\text{threshold}_{\text{diff}}$) for each participant between each movement condition and a respective baseline

condition (detection of the same probes at rest, see Fig. 2A). Positive values of $\text{threshold}_{\text{diff}}$ indicate stronger tactile suppression during movement. If tactile suppression stems from sensorimotor predictions, we expect stronger suppression (increased $\text{threshold}_{\text{diff}}$) in congruent than in incongruent conditions, as the probe frequencies would match the movement-related predictions. If, on the other hand, tactile suppression stems from an unspecific mechanism, then we should observe similar suppression across all movement conditions (comparable $\text{threshold}_{\text{diff}}$) (22).

Results

First, to determine whether tactile perception was affected during movement compared to rest, we performed two-tailed t tests against zero on $\text{threshold}_{\text{diff}}$. Data from a representative participant (Fig. 2A) show increased detection thresholds during movement compared to rest. In line with previous findings (16, 26), tactile probe stimuli were indeed suppressed in all movement conditions. Specifically, detection thresholds during movement were systematically larger than those at rest, indicated by all $\text{threshold}_{\text{diff}}$ being significantly greater than zero (low frequency congruent: $t[31] = 6.25$, $P < 0.001$, $d = 1.11$; low

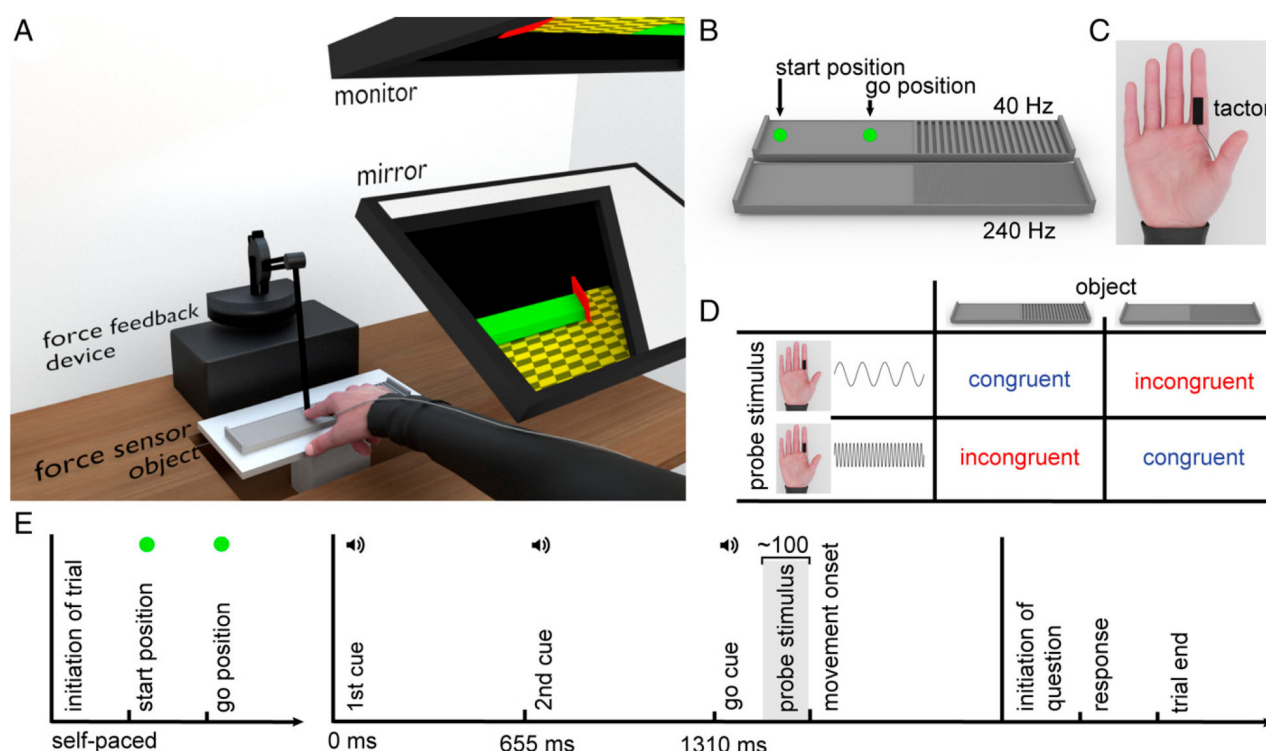


Fig. 1. Illustration of the experimental setup and design. (A) Participants were seated in front of a desk with the force sensor, the object and the force feedback device placed in front of them. A mirror blocked the view of the hand and the object. Participants viewed the scene presented to them on the monitor through the mirror. (B) The objects with two different textured surfaces that would cause the participant to experience a low fundamental frequency (40 Hz) and a high fundamental frequency (240 Hz), respectively. The start position at which participants initially made contact with the object and the go position from which participants began the stroking movements along the texture are marked with arrows. These two positions were represented to participants visually by green spheres on the monitor and were not discernible by touching the object. (C) The tactile stimulation device (tactor) was placed on the ventral part of the proximal phalanx of the right index finger. (D) The combination of the low frequency (40 Hz) and high frequency (240 Hz) objects with the two probe stimulation frequencies that either matched or mismatched the fundamental frequencies experienced by moving along the textured objects resulted in four movement conditions: low frequency congruent, low frequency incongruent, high frequency congruent, low frequency incongruent. (E) Participants initiated each trial via a central, virtual button. A green circle (start position) appeared at the very left of the object in the virtual workspace. Once participants moved their finger to the start position, thus touching the real object, the circle vanished and reappeared at the go position, 7 cm further to the right (~3 cm before the textured area). Participants moved their finger to this go position at their own pace. Once there, three auditory cues spaced 655 ms apart sounded, prompting participants to start a smooth continuous movement at the designated speed of 203 mm/s after the third cue (go cue). The probe stimulus was presented 100 ms before the anticipated movement onset. After reaching the end of the textured area, participants initiated the question about the tactile stimulus via a central, virtual button and responded with either “yes” or “no” by selecting the respective button.

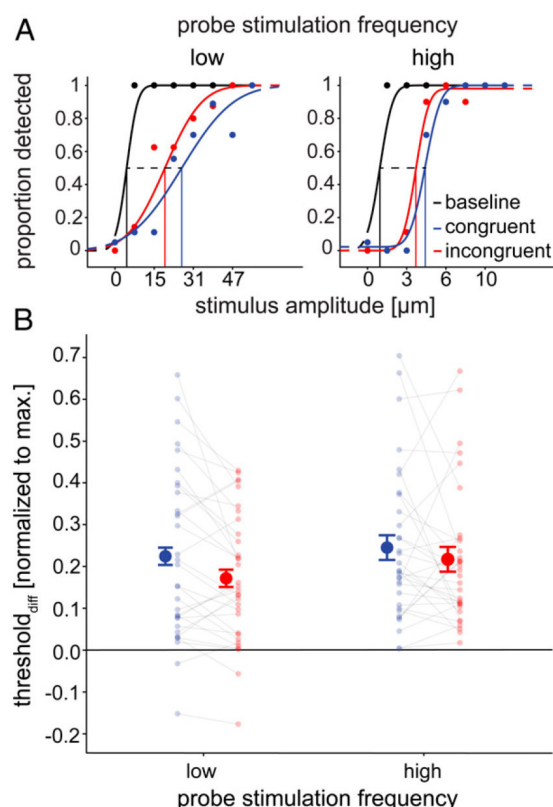


Fig. 2. The results of the tactile detection task. (A) Example psychometric functions of a single participant for low and high frequency probes. Each panel shows psychometric functions for the baseline and the congruent and incongruent movement conditions for the respective probe frequency. Some datapoints are not visible due to overlap. The difference between the baseline and the movement conditions is exemplified by the dotted line representing threshold_{diff} for both movement conditions. (B) Individual (transparent data points; $n = 32$) and mean differences in detection of the probe stimulation between the baseline and the movement conditions as measured by the change in detection thresholds, averaged across all participants. Threshold_{diff} represents the difference between the movement condition and the respective baseline condition (i.e., the suppression effect). Threshold_{diff} values are normalized to the maximum possible suppression at the respective probe frequency. Greater values indicate impaired sensitivity to probes (i.e., tactile suppression) in the movement conditions, while zero indicates no difference from the baseline. The error bars display 95% Cousineau-Morey confidence intervals for the difference between congruent and incongruent conditions within each probe stimulation frequency (27, 28). Tactile suppression took place in all movement conditions and was generally greater in congruent compared to incongruent conditions.

frequency incongruent: $t [31] = 6.24$, $P < 0.001$, $d = 1.10$; high frequency congruent: $t [31] = 7.61$, $P < 0.001$, $d = 1.35$; and high frequency incongruent: $t [31] = 7.39$, $P < 0.001$, $d = 1.31$ (Fig. 2B).

Second, we examined whether this suppression was stronger in congruent than incongruent conditions, which would provide strong evidence for the involvement of sensorimotor predictions. To this end, we compared threshold_{diff} using a 2 (probe frequency: low vs. high) by 2 (congruency: congruent vs. incongruent) univariate, repeated-measures ANOVA. Importantly, tactile suppression, as reflected in threshold_{diff}, was stronger for congruent compared to incongruent conditions (main effect of congruency, $F [1,31] = 5.35$, $P = 0.028$, $\eta_G^2 = 0.013$), whereas there was no effect of probe frequency ($F [1,31] = 0.91$, $P = 0.347$, $\eta_G^2 = 0.009$) nor an interaction ($F [1,31] = 0.47$, $P = 0.497$, $\eta_G^2 = 0.001$) (see Fig. 2B).

The congruency effect on suppression provides evidence for a strong sensorimotor prediction component. However, it may be contaminated by different response criteria across movement conditions. To control for this, we calculated for each movement condition performed by each participant the response criterion (according to signal detection theory, see *Materials and Methods* for details) (29), which we then submitted to a 2 (probe frequency: low vs. high) by 2 (congruency: congruent vs. incongruent) univariate, repeated-measures ANOVA. The results show that the response criterion did not significantly differ between conditions (mean $\pm$ SD: low frequency congruent = -1.89 ± 0.19 , low frequency incongruent = -1.88 ± 0.21 , high frequency congruent = -1.90 ± 0.15 and high frequency incongruent movement conditions = -1.90 ± 0.15), with neither significant main effects of congruency ($F [1,31] < 0.03$, $P = 0.855$, $\eta_G^2 < 0.001$) or probe frequency ($F [1,31] = 0.16$, $P = 0.690$, $\eta_G^2 = 0.002$), nor a significant interaction ($F [1,31] = 0.05$, $P = 0.831$, $\eta_G^2 < 0.001$). Thus, the increased thresholds_{diff} in congruent compared to incongruent conditions are unlikely to be explained by differences in the response criterion. The evidence for sensorimotor predictions is further corroborated by an additional analysis of the sensitivity measure d' (SI Appendix, Fig. S2) (29), which also demonstrates poorer sensitivity in congruent than incongruent conditions (SI Appendix, Signal Detection Analysis for further details).

Last, to test if the differences in threshold_{diff} between the movement conditions may be due to differences in the movement itself, rather than to a prediction of the sensory states, we compared several kinematic parameters using a 2 (probe frequency: low vs. high) by 2 (congruency: congruent vs. incongruent) univariate, repeated-measures ANOVAs. No statistically significant differences were found for the stimulation time (all $F [1,31] \leq 3.12$, $P \geq 0.087$, $\eta_G^2 \leq 0.013$), the reaction time (all $F [1,31] \leq 3.06$, $P \geq 0.090$, $\eta_G^2 \leq 0.002$), the movement duration (all $F [1,31] \leq 1.08$, $P \geq 0.307$, $\eta_G^2 \leq 0.005$), the average force exerted during the movement (all $F [1,31] \leq 3.10$, $P \geq 0.088$, $\eta_G^2 \leq 0.012$), the average movement velocity (all $F [1,31] \leq 1.56$, $P \geq 0.221$, $\eta_G^2 \leq 0.007$), the average acceleration (all $F [1,31] \leq 2.07$, $P \geq 0.161$, $\eta_G^2 \leq 0.008$), and the average deceleration (all $F [1,31] \leq 1.17$, $P \geq 0.287$, $\eta_G^2 \leq 0.003$) (SI Appendix, Fig. S5).

In summary, congruent vibrotactile probes matching the predicted sensations caused by the movement along textured objects were subject to stronger suppression than incongruent probes. No statistically significant differences in the response criteria or the movement kinematics were found across conditions, making the possibility of systematic biases or movement effects on the detection performance unlikely.

Discussion

Suppression of externally generated sensations shortly before and during voluntary movements is a well-established phenomenon (1, 14, 30). On one hand, it seems paradoxical to suppress sensations not caused by one's own actions since survival and adaptation require to enhance, and not to suppress, novel and potentially harmful sensations. On the other hand, a surge of somatosensory afferents from the moving limb could overwhelm the system, so it may be beneficial to suppress somatosensory feedback from that limb altogether, including external stimuli. Considering this, the functional mechanisms governing sensory suppression of external stimulations are still a matter of debate. Although this phenomenon has been attributed to predictive mechanisms, such as internal forward models (31), other

accounts claim that it stems from an unspecific mechanism, because the probe stimuli used to measure suppression cannot be predicted by an efference copy of the motor command itself (22, 23), or because backward masking may generally obscure any sensations on the moving limb (1). Here, we set out to address the debate on the origin of tactile suppression and show that tactile suppression of externally generated sensations originates from specific sensorimotor predictions.

We demonstrate that the well-established suppression of tactile sensations is stronger when the frequency of the probe stimulus's vibration matches the predicted vibration caused by the finger movement along the object's texture. In other words, suppression was stronger in the congruent than incongruent conditions as reflected in increased detection thresholds. This congruency effect cannot be attributed to a general cancellation policy that blankets any stimulus on the moving limb. It can neither be attributed to different response biases, nor to different kinematic performance across movement conditions, as our results show. Rather, a predictive mechanism is regulating the strength of suppression on the basis of specific sensorimotor predictions about the future sensory states generated by the movement.

We found elevated detection thresholds in all movement conditions compared to rest. This suppression effect is present in both congruent and incongruent conditions (i.e., unrelated to the congruency effect). Instead, it can be explained by sensorimotor predictions about the future state of the moving arm, which in turn leads to downweighted sensory processing around the movement (16, 30). As sensory feedback is subject to sensory noise and processing delays, predicting and, as a result discounting, such sensations can be advantageous and possibly desired (31). We suggest that the observed suppression effect comprises two components: one that originates from sensorimotor predictions about the sensory states of the moving arm, and a second one caused by the congruency between the probe stimulation and the predicted sensory consequences of the stroking movement.

Motor control theories involving feedforward control can account for tactile suppression (31, 32). Sensorimotor control is thought to depend on the optimal integration of a sensorimotor estimate about the future sensory states of the system and of peripheral sensory input (33). When the state of one's own sensory system is uncertain, sensory feedback is downweighted and reliance on sensorimotor estimates is greater (34). Accordingly, in the presence of sensorimotor predictions, sensory feedback, including any external probes, is downweighted to different extents, depending on the reliability of the prediction. This is reflected in attenuated activity in central brain regions, such as sensory and motor cortices, to tactile probes on a limb shortly before its movement (18, 19). Tactile suppression of external probe stimuli is also modulated by feedback demands, such that it is weaker when task-relevant feedback gains importance (14–16) and stronger when movement feedback becomes more predictable (35). This suggests that suppression depends on a dynamic interplay between predictive and feedback signals (11). However, to the best of our knowledge, no study hitherto has distinguished whether this suppression is based on predictive mechanisms, leaving the phenomenon open to different interpretations. One such interpretation is that tactile suppression of external probes is caused by unpredictable mechanisms, such as backward masking of the probe stimuli by peripheral reafferences from the moving limb. Although backward masking may influence sensory processing briefly before and during the movement (1, 21), it does not

always occur (11). Masking might have contributed to the generally elevated detection thresholds we observed during movement, however, we presented the probe stimuli well before movement onset (on average 119 ms before), which is substantially earlier than the time window of backward masking (~50 ms before movement onset) (20, 35). Probes were also presented well before touching the object's texture (at least 250 ms), which far exceeded the threshold of temporal tactile acuity (50–70 ms) (36), allowing for the perception of the probe stimulation and the texture as two distinct events. Importantly, the differences between the congruent and incongruent conditions can neither be explained by backward masking, nor by any other movement-related mechanism (35, 37, 38), as kinematic behavior was also similar between conditions.

Tactile suppression has also been discussed in the context of the opposing process theory (22), according to which predicted sensations may first be enhanced and later cancelled should unexpected sensations arise. This theory is based on the premise that tactile suppression does not differ between expected and unexpected sensations and is hence not predictive. Here, we show that exafferent tactile probes matching predicted sensations are suppressed more strongly than mismatching probes. Importantly these probes themselves are not the subject of precise sensorimotor predictions; instead, sensorimotor predictions are made about the sensory states associated with the movement (i.e., the vibrations caused by moving the finger across the textured objects). Critically, the exafferent stimulations can be used to probe the sensory suppression effect of those predictions. While our experiment was not designed to evaluate the opposing process theory directly, it is inconsistent with both our results and previous work from the tactile domain showing predictive suppression of self-generated (39) and externally generated tactile sensations (10, 12, 14) occurring up to 300 ms before movement onset (i.e., lacking preceding enhancement).

In sum, we conclude that tactile suppression of externally generated stimuli on a moving limb is modulated in a highly specific manner, as it is stronger when the generated stimuli match the predicted sensory feedback. This speaks in favor of sensorimotor predictions involved in tactile suppression. Our findings provide evidence for the origins and underlying mechanisms of tactile suppression and form the ground to unify the processes that govern sensory tuning, also in other modalities, such as vision (40–42 but see also 43) and audition (see 44 for a review). This contributes to a better understanding of the computational principles and neurobiological substrates of human sensorimotor control as well as of clinical phenomena related to predictive mechanisms, such as Parkinson's disease (45), obsessive-compulsive disorder (46), schizophrenia (47, 48), and depression (49).

Materials and Methods

Participants. A total of 48 participants completed the experiment and were compensated with either course credit or a payment of 8€/h. Due to exclusion criteria listed below, 32 participants (23 women, 9 men, range 19–30 y, 22.56 ± 3.03) were included in the final sample (see *Quantification and Statistical Analysis* for the exclusion criteria; *SI Appendix, Fig. S4* for psychometric functions of all 48 participants; *SI Appendix* for the sample size considerations). The experiment was approved by the local ethics committee at the Justus Liebig University Giessen and was in accordance with the Declaration of Helsinki (2013). All participants provided their signed informed consent. Participants were right-handed according to the German translation of the Edinburgh Handedness Inventory (50) (77.94 ± 21.48). Furthermore, participants reported no current neurological symptoms, no issues with stereopsis or color vision, and had normal or corrected to normal eyesight. Participants also did not report any injuries to the right index

finger and had a two-point-discrimination threshold of at least 3 mm on the right index finger ($2.34 \text{ mm} \pm 0.48 \text{ mm}$; Two-Point Discriminator, North Coast Medical).

Apparatus. To assess tactile suppression, a vibrotactile stimulation device (PiezoTac tactor; skin contactor diameter 6.4 mm; Engineering Acoustics) was attached to the ventral part of the proximal phalanx of the participants' right index finger and was secured with medical tape. The tactor encompassed a skin contactor mounted on a shielded cantilever. Vibrations of the cantilever produced sinusoidal contactor oscillations perpendicular to the skin. We presented brief (100 ms) vibrotactile probes of eight varying oscillation amplitudes for each of the two probe frequencies that we used (40 Hz; 240 Hz). The peak-to-peak displacements of the oscillations ranged from 0 (no stimulation) to $54.45 \text{ }\mu\text{m}$ and to $11.31 \text{ }\mu\text{m}$ (*SI Appendix*) for probe frequencies of 40 Hz and 240 Hz, respectively. These displacements were identical in the baseline and movement conditions. White noise was played through over-ear-headphones to prevent participants from hearing the sound caused by the vibrotactile stimulation.

The textured objects ($209 \times 40 \text{ mm}$) were printed using a three-dimensional (3D) PolyJet printer (Stratasys; Objet30 Pro; printing resolution: 600–1600 dpi; material VeroClear). The right half of the object had a texture with an even cube-wave pattern. The left half of the object was smooth to mitigate the risk of participants adapting to the texture over time. To create two distinct objects, a texture with a high spatial period of 5.08 mm and another one with a smaller spatial period of 0.85 mm were chosen. When moving along these textures at a constant velocity of 203 mm/s (average recorded speed $203 \pm 35 \text{ mm/s}$, range: 110–329 mm/s; *SI Appendix, Fig. S6* for further details), these spatial periods elicited vibrations with frequencies of 40 Hz and 240 Hz, respectively, on the participants' fingertip (see Fig. 1*B*). Two types of mechanoreceptors were targeted with these vibration frequencies to ensure the prediction of discrete sensory states. With frequencies of 40 Hz we mainly stimulated the Meissner corpuscles that have a receptive range of 10–100 Hz and are most sensitive to vibrations of 40–60 Hz (24, 25). The probes of 240 Hz lie in the response range of the Pacinian corpuscles reaching from 40 to 800 Hz (24), with their maximal sensitivity being between 200–300 Hz (25). While moving the finger along the textures may result in a complex set of vibrotactile sensations that go beyond a single frequency, we expect that the experienced vibrations are dominated by a fundamental frequency that follows the spatial frequency of the textured surface, along with some weaker noise and harmonic components (51) (*fundamental temporal frequency = spatial frequency * velocity*).

The experiment was conducted using a 3D virtual environment, wherein the position of the participants' index finger as well as the exerted forces were collected through a force feedback device (PHANTOM 1.5A, 3D Systems) and a force sensor (bending beam load cell LCB 130 and a measuring amplifier GSV-2AS, resolution 0.05 N, ME-Messsysteme GmbH). Custom-made software (C++) was used to run the experiment, collect responses, and record the force and finger position every 3 ms. Participants sat in front of a table and connected their hand to the force feedback device using a custom-made plastic fingernail which was attached to the nail of their index finger with moldable adhesive pads. This setup allowed keeping the finger pad free for haptic exploration. Participants had no view of their finger connected to the force feedback device or the objects and instead viewed a spatially aligned 3D representation of the scene on a 22" monitor (120 Hz, $786 \times 1024 \text{ pixel}$) by looking through a mirror using a pair of stereo glasses (3D Vision 2, NVidia). Visual information associated with experimental control, such as questions and answers for the detection task, were presented on the monitor and corresponded to specific virtual positions in the workspace. Participants could navigate through the experiment and indicate answers by moving their finger and thus the force feedback device to those virtual buttons.

Procedure. The experiment consisted of a sequence of five blocks, one for each movement condition (2 probe frequencies * 2 object frequencies), and one for the baseline condition. To familiarize participants with the use of the force feedback device and the nature of the tactile stimulations, they first performed 20 mock trials of the baseline condition. These data were not included in the analysis. Next, half of the participants continued with the baseline condition while the other half completed the baseline at the very end of the experimental session. Before the start of the first block of the movement condition, participants

performed two practice blocks to train their movement along a smooth object at the designated speed. Before the second, third, and fourth block of the movement condition, they performed one practice block of eight trials (*SI Appendix* for details on the practice trials). The order of the four movement conditions was pseudorandomized with a Latin square design resulting in four possible sequences, with each condition being equally likely to occur at each position.

Participants were seated in front of a desk with the force sensor, the object and the force feedback device placed in front of them. A mirror blocked the view of the hand and the object. Participants viewed the scene presented to them on the monitor through the mirror. To probe tactile perception, a brief vibrotactile probe was delivered to the participants' index finger in both movement and baseline conditions. At the end of each trial, participants were to respond whether they detected the probe or not. To limit the possibility of a response criterion shift between the conditions, the experimenter instructed the participants to adopt a conservative response criterion before each block of the baseline and movement conditions. For each probing frequency, we presented 70 trials with stimulation (each of the seven stimulation amplitudes repeated 10 times) and 20 trials with no stimulation in a randomized order. This resulted in a total of 90 trials for each block of the movement condition and 180 trials for the block of the baseline condition that involved both probe frequencies.

In each of the four movement conditions, the participants' right index finger was attached to the force feedback device. They were to move their finger along the textured objects at a constant speed of 203 mm/s while detecting the vibrotactile probes (see Fig. 1 for further details). If participants deviated considerably from the prescribed movement, the software repeated the respective trials and the experimenter gave feedback (*SI Appendix* for further details). To avoid any influence of the textured object and/or the movement itself on tactile suppression, we presented the probe stimuli shortly before the anticipated movement onset, specifically 100 ms before the median reaction time of the preceding five trials (19, 37). For the first five trials, the stimulation was presented 150 ms after the go cue. Upon initiating the trial by moving to a virtual button, a schematic representation of the object's left and right outer borders was presented, along with a green circle at the very left of the object (start position). As soon as participants moved their right finger to that circle, thus touching the real object in the workspace, the circle vanished and reappeared at the go position, 7 cm further to the right ($\sim 3 \text{ cm}$ before the textured area). Participants moved their finger at their own pace to that new position while keeping contact with the object. To prevent participants from drifting back again after having reached the go position, a force "wall" was generated by the force feedback device to the left of this point. Once participants reached the go position, an untextured green block representing the remaining right part of the object appeared on the monitor followed by three auditory cues spaced 655 ms apart. This time interval of 655 ms corresponded to the time participants needed to travel the complete remaining distance of the object at an average speed of 203 mm/s and thus aided the participants to adhere to this designated speed. Accordingly, participants started a smooth, continuous movement with the last of the three consecutive auditory cues (go cue) and had to finish their movement at the time of an imagined fourth cue. Once they reached the end of the textured area, the object's visual representation disappeared, and participants could initiate the detection question about the tactile stimulus via a central virtual button and responded with "yes" or "no" by selecting the respective virtual button with the right index finger.

The baseline condition served to determine each individual's tactile detection performance for each probe frequency at rest. Participants placed their right hand comfortably on the table in front of them while the finger with the tactor rested on a pad to avoid the vibrations from reverberating through the table and distorting the measurement. In the baseline condition only, the participants' left index finger was attached to the force feedback device to control the experiment in order to limit possible effects on tactile perception from subsequent movements of the stimulated hand. Participants started each trial by bringing their left finger to a virtual button. After 100 ms, a probing tactile stimulus was delivered to their right index finger followed by a delay of 500 ms. Then, a question asking whether the participants had felt a vibration was presented on the virtual monitor and could be answered as during the movement condition. Throughout the baseline condition, the right hand remained completely stationary.

Quantification and Statistical Analysis. The kinematic data were processed using MATLAB R2021a (The MathWorks) (*SI Appendix* for further details). To

avoid any possible effects of backward masking by the texture, only trials in which the stimulation ended at least 150 ms before participants reached the texture were included in the analysis of the tactile detection task (20, 21, 35, 52). Likewise, only trials with stimulations starting no earlier than 300 ms before movement onset were included, to avoid probing suppression at a moment that is too early to occur (10, 14). Based on these criteria, $88 \pm 8\%$ of trials were included on average per participant and movement condition (SI Appendix, Fig. S3 for detection thresholds derived without trial exclusion). One participant was excluded because less than 60% of the trials remained based on the two above-mentioned criteria. The average timespan between stimulation onset and the moment when the finger reached the texture was 360 ± 25 ms, while the probing stimulus was presented on average 119 ± 14 ms before movement onset. Thus, our probing stimuli were presented during the time window when tactile suppression already occurs (10, 14) (SI Appendix, Fig. S1).

Cumulative Gaussian functions were fitted to the responses of the tactile detection task, using the maximum likelihood procedure implemented in the psignifit 4 toolbox (53) for MATLAB. Separate functions were fitted for each of the four movement conditions and each participant. Two additional psychometric functions were fitted for responses to the low and the high frequency probes of the baseline condition. A technical issue erroneously changed the first period of the sinusoidal oscillation for trial n to the probe frequency of the trial $n-1$. This obviously does not affect the probes presented during the movement conditions, as each block of the movement condition only included a single probe frequency. However, since the two probe frequencies were intermixed randomly in the baseline condition, the frequency was mingled in some trials. To account for this, we fit baseline psychometric functions by using only those trials that had the same probe frequency as the trial before ($50 \pm 3\%$ and $50 \pm 4\%$ for low and high probe stimulation frequency). Importantly, the exact strength of

suppression in all movement conditions was affected equally. For each of the psychometric functions, we calculated the detection threshold as the stimulus amplitude that had a 50% probability of being detected. To account for differences across individual baseline detection sensitivities, we subtracted each participant's baseline detection threshold from the respective value of each of their movement conditions, separately for low and high frequencies. This resulted in four threshold_{diff} values per participant, with higher values representing stronger suppression during movement compared to rest. To rule out any poorly fitted data, participants with detection thresholds exceeding the range of stimulation ($n = 9$) or with false alarm rates of 20% or more ($n = 6$) were excluded. The response criterion was calculated separately for each condition and each participant as the z-transformed false alarm rate (29). Rates of 0 and 1 were corrected to $\frac{0.5}{n}$ and $\frac{n-0.5}{n}$, respectively, with n being the number of no stimulation trials (54). Averages are reported as mean $\pm$ SD throughout the manuscript. The statistical analyses were carried out with a significance level of $\alpha = 0.05$ using R (R Foundation for Statistical Computing). Effect sizes are reported as Cohen's d for t tests and as generalized Eta squared for ANOVAs. Cohen's d was calculated as the difference between the means divided by the SD of the difference.

Data Availability. Anonymized data have been deposited in Open Science Framework (DOI: [10.17605/OSF.IO/G5ZBJ](https://doi.org/10.17605/OSF.IO/G5ZBJ)).

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3 Study II: Characterizing SEPs from Pacinian-targeted vibrations

RESEARCH ARTICLE

Sensory Processing

Characterizing SEPs from Pacinian-targeted vibrations

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Abstract

This study characterizes short- and long-latency somatosensory-evoked potentials (SEPs) elicited by high-frequency vibrotactile stimuli. Unlike conventional electrical stimulation, such vibrations selectively recruit Pacinian corpuscles while sparing other mechanoreceptors, motor, proprioceptive, and nociceptive fibers, thereby offering a more ecologically valid proxy for natural touch. We first show that SEP components P45, P100, N140, P200, and P300 scaled systematically with vibration amplitude, and quantify the increase in SEP voltage per increase in peak-to-peak vibration amplitude for suprathreshold stimuli. We then compare vibrotactile SEPs to those produced by perceptually matched electrical stimulations given at the same finger location. The overall morphology of vibrotactile SEPs at contralateral electrode CP3 appeared similar to electrical SEPs from the P45 and onward. However, short-latency components P45 and N70 revealed distinct scalp topographies, indicating different cortical sources for the two stimulation modalities. Source analysis revealed greater early activation (~45 ms) of contralateral primary somatosensory regions whereas posterior parietal areas and SII showed differential activation for vibrations and electrical stimulations. Later processing and integration of sensory information recruited similar neural sources for both modalities. These findings offer a comprehensive reference for SEP responses to Pacinian-targeted vibrations and highlight the use of naturalistic stimuli in human somatosensory electrophysiology.

NEW & NOTEWORTHY Somatosensory-evoked potentials (SEPs) are commonly studied using transcutaneous nerve stimulation, which does not reflect the selective engagement of mechanoreceptors in natural touch. Here, we use naturalistic vibrotactile stimuli to selectively target Pacinian mechanoreceptors. We quantify the scaling of short- and long-latency SEPs with vibration amplitude and uncover key differences from electrically evoked responses. This work enhances the ecological validity of SEP research and provides a framework for studying neural responses to real-world touch.

Pacini-corpuscles; somatosensory-evoked potentials (SEPs); source localization; stimulation intensity; vibration

INTRODUCTION

Somatosensory-evoked potentials (SEPs) are commonly investigated in clinical and research settings using transcutaneous electrical nerve stimulation, which elicits a range of short- and long-latency components (1). Electrical stimuli are typically applied at the upper limb to stimulate the median or ulnar nerve at the wrist or thumb. These nerves consist of A α motor fibers, A β sensory fibers that transmit tactile and proprioceptive information, A δ fibers that carry nociceptive and thermal sensations, and unmyelinated C fibers transmitting prolonged nociceptive sensations or affective touch (2). A β fibers include two subtypes of rapidly adapting fibers with distinct nerve endings: RAI fibers, which

carry low-frequency vibration information from Meissner corpuscles, and RAII fibers, which transmit signals from Pacinian corpuscles (3). In addition, there are two subtypes of slowly adapting fibers: SAI fibers, associated with Merkel's disks for sensing static skin indentation, and SAII fibers, linked to Ruffini endings for coding skin stretch (2). Unlike natural touch, transcutaneous nerve stimulation bypasses these nerve endings and directly excites the axons of all A β fiber subtypes along with A α fibers simultaneously (4). More intense stimulations also activate A δ fibers, eliciting sharp nociceptive sensations (5).

Although electrical stimulation yields clear SEPs, the evoked spatial pattern of multiple fiber types in different layers of the skin is broader than during natural mechanical



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stimulation (6). Likewise, the temporal pattern of electrical stimulation is unnatural, with single impulses in many fibers rather than multiple discharges in selective fiber subtypes (6). Thus, electrical stimulations evoke a unique sensation unlike any naturalistic touch, limiting behavioral research. In addition, participants may experience electrical stimulations as unpleasant, making the method less suited to cognitive neuroscience research in children, older adults, or patients. Mechanical stimulations such as vibrations (7), skin indentations (8), air puffs (9), or slip motion (10) provide a more naturalistic alternative used in behavioral somatosensory research (for a review of methods and devices see Ref. 11). The amplitude of mechanical stimulation can be increased without the concern of reaching motor- or pain-threshold, making it more suitable for research involving movements or psychophysical tasks. In addition to offering a more naturalistic touch pattern, mechanical stimulations can be applied anywhere on the body and can excite A β fiber subtypes more selectively by targeting specific mechanoreceptors. The parameters of vibrations can be finely adjusted in terms of amplitude, frequency, and duration to allow for a wide range of sub- or suprathreshold stimulations necessary for psychophysical research. Compared with air puffs, vibrations delivered via skin contactors are also possible to use during movements like reaching (12) or grasping (13).

Although vibrations are a useful tool for electrophysiology research, detailed comparisons between SEPs elicited by vibration and electrical stimulation remain scarce. As with electrical median nerve stimulation (14, 15), vibrotactile stimulations of varying intensities have been shown to result in SEP amplitude modulations (16). Although vibrotactile stimulation intensity effects on the P200, associated with tactile attention, and the P300, linked to general attention processing, are known (17), their influence on earlier SEPs such as the P45, N70, P100, and N140 remains unclear. One notable distinction to electrical stimulation is the absence of early components occurring before 50 ms following vibrations (17, 18). The lack of short-latency potentials may stem from a combination of factors, such as the small voltage of those SEPs, the lower intensity of vibrations compared with electrical stimulations, low sampling rates, few trial repetitions (16), and small sample sizes used in previous studies (18).

To facilitate electrophysiological research using vibrotactile stimulation, we characterize SEPs following vibrations that selectively target Pacinian corpuscles and RAI fiber types. Specifically, we examine SEP changes across different vibration amplitudes for both short- and long-latency components. We hypothesize that SEPs will scale with vibrotactile stimulation intensity. In addition, we compare SEPs evoked by vibrations to those elicited by electrical stimulation at the same finger location.

METHODS

Participants

Thirty-four participants (self-reported gender: 23 females, 11 males; mean age = 24.5 yr, SD = 3.9) provided signed informed consent and were compensated with either course

credit or 10 €/h. The experiment was approved by the local ethics committee at the Justus Liebig University Giessen and conducted in accordance with the Declaration of Helsinki (19), except of preregistration. Participants were right-handed according to the German translation of the Edinburgh Handedness Inventory (20; mean = 95.8, SD = 8.9) and reported no neurological or psychiatric conditions. Two participants were excluded due to either moving their right hand during the experiment or excessive skin potentials observed in the EEG recording. A subset of 19 participants who took part in the vibrotactile experiment also received electrical stimulations (14 females, mean age = 24.9 yr, SD = 3.5) on a different day. One participant received vibrotactile stimulations first, followed by electrical stimulations in the same session with a 30-min break in between. Another participant completed only the electrical stimulation.

Material and Procedure

A vibrotactile stimulation device (PiezoTac tactor; skin contactor diameter 6.4 mm; Engineering Acoustics Inc., Casselberry, FL) was attached to the palmar side of the proximal phalanx of the index finger to facilitate future investigations of somatosensory perception during finger movements, as this positioning keeps the fingertip unobstructed. The tactor consisted of a skin contactor mounted on a shielded cantilever. Vibrations of the cantilever generated sinusoidal oscillations perpendicular to the skin. Each participant received 200 repetitions each of sinusoidal vibrotactile stimulations (20 ms, 280 Hz) at four suprathreshold amplitudes in randomized order. The vibrations had peak-to-peak displacements of 42, 97, 134, and 190 μ m according to the manufacturer's (Engineering Acoustics Inc., Casselberry, FL) specifications for the actuator at the given frequency and driving voltage. These amplitudes started at a weak but suprathreshold level and covered a range of intensities consistent with previous psychophysical studies (12, 21, 22). Participants wore earplugs to mask vibration noise. Electrical stimulations were given using two DS7A stimulators (Digitimer Ltd., Hertfordshire, UK) connected to a surface electrode (bar electrode, distance 30 mm; GVB-geliMED, Bad Segeberg, Germany). The electrode was attached to the first two proximal phalanges of the participant's right finger with medical tape, covering the location of the vibrotactile stimulation. Constant current square wave pulses were delivered at 350 V with a duration of 2 ms and four intensities (0.91, 1.15, 1.29, and 1.41 mA) repeated 200 times each.

This protocol represents a deliberate deviation from standard electrical median nerve stimulation, which typically targets the main nerve branch at the wrist to elicit a thumb twitch and calibrate stimulation intensity based on motor threshold (4). In our study, both stimulation types were applied to the palmar side of the proximal phalanx of the index finger, innervated by two palmar branches of the median nerve (23). The electrode was positioned centrally on the finger, engaging smaller nerve ramifications rather than the main trunk. To enhance perceptual comparability between the two stimulation types, we also adjusted the electrical stimulation parameters by using longer pulses

and interstimulus intervals than are common in median nerve stimulation (4, 24, 25). Electrical stimulation intensities were selected to match the perceived strength of vibrations, based on a separate pilot study with eight participants (four females, mean age = 23.9, SD = 4), six of whom also participated in the main experiment (see Supplemental Material for further information).

The stimulation devices were controlled using custom Python (v.3.8.13; RRID:SCR_008394) code and the PsychoPy software package (v.2022.1.1; RRID:SCR_006571; 26). Because vibration and electrical pulses were generated by separate devices, we quantified each device's trigger-to-stimulus delay to account for it during preprocessing of the EEG data. Vibrotactile delay (mean = 5.6 ms, SD = 0.78) was measured in a single test run of the experiment using a StimTrak and audio adapter (BrainProducts, Gilching, Germany) with a contact microphone fixed to the skin contactor. Electrical-stimulator delay (DS7A; Digitimer Ltd., Hertfordshire, UK) was estimated from the stimulation artifact in the averaged vertical electrooculogram trace, appearing 2 ms after stimulation trigger onset. Participants sat with their hands resting on a table while fixating a cross at the center of a computer screen. They were instructed to attend to the stimulations of varying intensities presented in randomized order. Self-paced breaks were offered after every 50 trials. The order of the four vibrotactile stimulation amplitudes was randomized within each block. Since the electrical stimulation intensities had to be preset manually on the two stimulators, electrical stimulations were delivered in a blocked manner, grouping the two lower and the two higher intensities. Within each block, the two intensities were presented in randomized sequence, and the order of the low and high intensity blocks was counterbalanced across participants. The interstimulus-interval for all stimulations was 2.2 s. Each testing session included 800 trials and lasted ~30 min.

EEG Recording and Signal Processing

EEG signals were recorded using 64 active Ag/AgCl electrodes (actiCap), a BrainAmp system, and BrainVision Recorder software (all from BrainProducts, Gilching, Germany) at a sampling rate of 1 kHz. Electrodes were positioned according to the 10-20 system with two reference electrodes on the earlobes, additional electrodes on the outer canthi of both eyes, and one electrode underneath the right eye to monitor eye movements. One electrode (AF4) was removed due to technical issues. Impedances were maintained below 20 k Ω . The data were preprocessed using eeglab (v.2024.2; RRID:SCR_007292; 27) in MATLAB (R2021a; The MathWorks Inc., Natick, MA). Stimulation triggers were latency-corrected by 5 ms for vibrotactile stimulations and 2 ms for electrical stimulations. Preprocessing steps included correcting for the stimulation latency, applying a high-pass filter (noncausal Butterworth impulse response function, half-amplitude cut-off at 0.1 Hz, 12 dB/oct roll-off), removing DC offsets, and removing 50 Hz line noise using zapline plus (28). All electrodes were re-referenced offline to the average of the linked earlobes. Noisy channels were interpolated after visual inspection. Independent component analysis (ICA) was performed using the Infomax algorithm, with PCA rank reduction applied if channel interpolation had been required.

Eye artifacts were removed using independent component analysis and ICLabel (29). Additional artifacts were addressed using artifact subspace reconstruction. Epochs were extracted from -200 to 400 ms around the onset of the stimulation, and baseline-corrected using a 200 ms prestimulation period. The data were low-pass filtered (noncausal Butterworth impulse response function, half-amplitude cut-off at 40 Hz, 12 dB/oct roll-off). Averages were computed for each stimulation type (vibrotactile/electrical) and intensity. Component windows were defined around the peaks identified in the grand-averaged data.

Statistical Analysis

The analysis included an average of 180 (SD = 26.9) trials per vibrotactile stimulation amplitude and 182 (SD = 16.8) trials per electrical stimulation intensity per participant. Data were analyzed in eeglab (v.2024.2; RRID:SCR_007292; 27) using the Benjamini-Hochberg method to control the false discovery rate and adjust *P* values for multiple testing (30) when examining the influence of stimulation intensity on SEPs and when comparing vibration to electrical stimulation. Results were considered statistically significant at $P_{FDR} \leq 0.05$. We focused on CP3 over primary somatosensory cortex (SI) contralateral to the stimulation to identify SEPs. For a comprehensive comparison of SEPs stemming from vibrations versus electrical stimulation, we ran paired, two-tailed *t* tests on each individual channel. Effect sizes are reported as Cohen's d_z for paired sample *t* tests (31). To assess the relationship between stimulation intensity and SEP component amplitudes, we fitted linear mixed-effects models (LMMs) using restricted maximum likelihood estimation with the lmer() function from the lme4 package (32) in R (v.4.3.3; RRID:SCR_001905; 33). *P* values were computed using the Satterthwaite approximation as implemented in the lmerTest package (v.3.1.3; RRID:SCR_015656; 34). LMMs, like linear regression, can handle continuous independent variables, whereas ANOVAs categorize them into discrete levels. This allows LMMs to not only test whether changes in the independent variable influence the dependent variable but also directly estimate the magnitude of this effect through β coefficients (32, 35) rather than relying on separate post hoc calculations. Unlike linear regression, LMMs account for dependent data, making them particularly suitable for repeated-measures designs. They achieve this by modeling participant variability as random effects while treating variability from the independent variable as fixed effects (36). Thus, although ANOVAs can only test for a main effect of stimulation intensity, requiring additional post hoc tests to compare individual intensities, LMMs not only assess whether stimulation intensity significantly influences SEP amplitudes but also provide direct estimates of how much SEP amplitudes change with varying stimulation intensity. For the LMMs, normality of residuals was assessed via Q-Q plots, which showed no substantial deviations from linearity. Residuals plotted against fitted values showed no indication of heteroscedasticity.

Source Localization

The SEP differences between vibrotactile and electrical stimulation observed in the P45 and N70 components were

further explored using cortical source estimation with minimum norm imaging using Brainstorm (v.3.250501; RRID: SCR_001761, 37) in MATLAB (R2021a; The MathWorks Inc., Natick, MA). Following the methods outlined by Stropahl et al. (38), we imported the preprocessed EEG data into Brainstorm and aligned the sensors to the default template anatomy. Brainstorm re-referenced the data to an average reference. Single-trial data were averaged for each stimulation type and participant, and distributed cortical source activity was estimated from these averages. Since conditions were recorded in separate sessions, single-subject noise covariance matrices were computed separately for each stimulation type, using the 200-ms prestimulus baseline. We observed activation in the left hemisphere contralateral to the stimulation around the central sulcus as well as in pre- and postcentral regions and along the lateral fissure. Ipsilateral activation in the right hemisphere was negligible and therefore not considered for the analysis. Regions of interest (ROIs) were defined according to the Destrieux Atlas (39) integrated in Brainstorm. Because the Destrieux atlas does not cover regions associated with the secondary somatosensory cortex (SII) adequately (40), we defined an additional left-hemispheric ROI that followed the activation cluster on the upper bank of the lateral fissure. To capture activity in neighboring areas, we also added the insula and the transverse and superior temporal cortices from the Desikan–Killiany atlas (41), eliminating any vertices that overlapped with our Destrieux regions (see Supplemental Table S1 for custom ROI coordinates).

ROIs were selected in two steps: first, group-level source maps for the P45 and N70 windows were visually inspected (see Fig. 3), and every cortical surface region showing activation in either stimulation type was flagged as a candidate ROI. For each candidate, mean source activation was extracted per modality and component. Regions whose mean amplitude reached $\geq 50\%$ of the grand mean across

all regions for at least one modality were retained. For the P45, this included precentral regions (inferior frontal sulcus, inferior and superior parts of the precentral sulcus, precentral gyrus), the central sulcus, postcentral regions (postcentral gyrus, postcentral sulcus, supramarginal gyrus, superior parietal lobule, intraparietal sulcus, and transverse parietal sulci), and temporal regions (upper bank of the lateral fissure, posterior segment of the lateral fissure, transverse temporal cortex). For the N70, we retained precentral regions (superior frontal sulcus, inferior and superior parts of the precentral sulcus, precentral gyrus), the central sulcus, postcentral regions (postcentral gyrus, intraparietal sulcus and transverse parietal sulci, supramarginal gyrus), and temporal regions (upper bank of the lateral fissure, posterior segment of the lateral fissure, insula, transverse and superior temporal cortices). Second, the retained ROIs were validated by paired, two-tailed t tests against the prestimulus period (-200 to 0 ms; see Supplemental Table S2). Only ROIs with significant activation were subjected to the final paired, two-tailed t tests comparing vibration and electrical stimulation within each component (see Table 1). When source activation data violated normality assumptions (Shapiro–Wilk test), we used the Wilcoxon signed-rank test instead and report effect-size as r (42). P values are reported as P_{FDR} with FDR correction (30) applied to account for testing multiple ROIs within each component against the prestimulus period and comparing activation between the two modalities.

RESULTS

To examine the effects of vibrotactile stimulation intensity on each ERP component, we computed the mean component amplitudes for the P45 (45 ± 5 ms), N70 (69 ± 5 ms), P100 (93 ± 5 ms), N140 (139 ± 5 ms), P200 (210 ± 10 ms), and P300 (279 ± 10 ms) at CP3. See Fig. 1A for the CP3 waveform and Fig. 1B for the corresponding topographies. Higher

Table 1. Comparison of mean source activity within ROIs in the left hemisphere during the time range of the P45 (42–52 ms) and N70 (64–74 ms) between vibrotactile and electrical stimulation

	$t(18)$	P_{FDR}	d_z	Significance
P45				
Inferior frontal sulcus	−2.95	0.0140	−0.68	*
Inferior part of the precentral sulcus	−2.44	0.0296	−0.56	*
Superior part of the precentral sulcus	−2.12	0.0484	−0.49	*
Precentral gyrus	2.12	0.0484	0.49	*
Central sulcus	−4.56	0.0016	−1.05	**
Postcentral gyrus	3.16	0.0119	0.72	*
Postcentral sulcus	5.39	0.0005	1.24	***
Supramarginal gyrus	4.04	0.0025	0.93	**
Intraparietal and transverse parietal sulci	2.86	0.0151	0.66	*
Superior parietal lobule	3.01	0.0139	0.69	*
Posterior segment of the lateral fissure	3.24	0.0118	0.74	*
Upper bank of the lateral fissure	2.46	0.0296	0.56	*
Transverse temporal cortex	−4.14	0.0025	−0.95	**
N70				
Postcentral sulcus	−2.12	0.1554	−0.49	
Insula	0.96	0.6240	0.11	
	W	Z	P_{FDR}	r
Superior frontal sulcus	134	1.57	0.1554	0.36
Superior temporal cortex	135	1.61	0.1554	0.37

All regions are located in the left hemisphere contralateral to the stimulation. ROI, regions of interest. Values are test statistics from paired-samples t tests (t , Cohen's d_z) and Wilcoxon signed-rank tests (W , Z , r). r , effect size; W , Wilcoxon test statistic; Z , standardized test statistic. P values are corrected for testing multiple regions within each component (30). *** $P_{\text{FDR}} < 0.001$, ** $P_{\text{FDR}} < 0.01$, * $P_{\text{FDR}} < 0.05$.

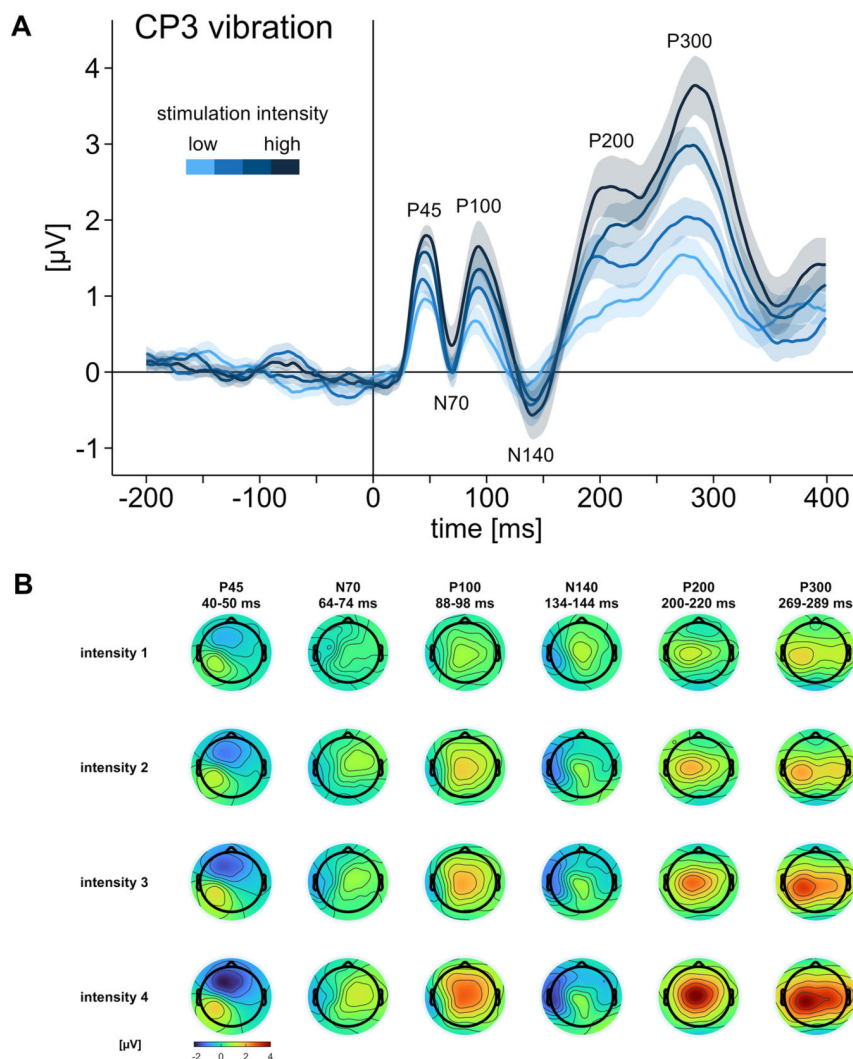


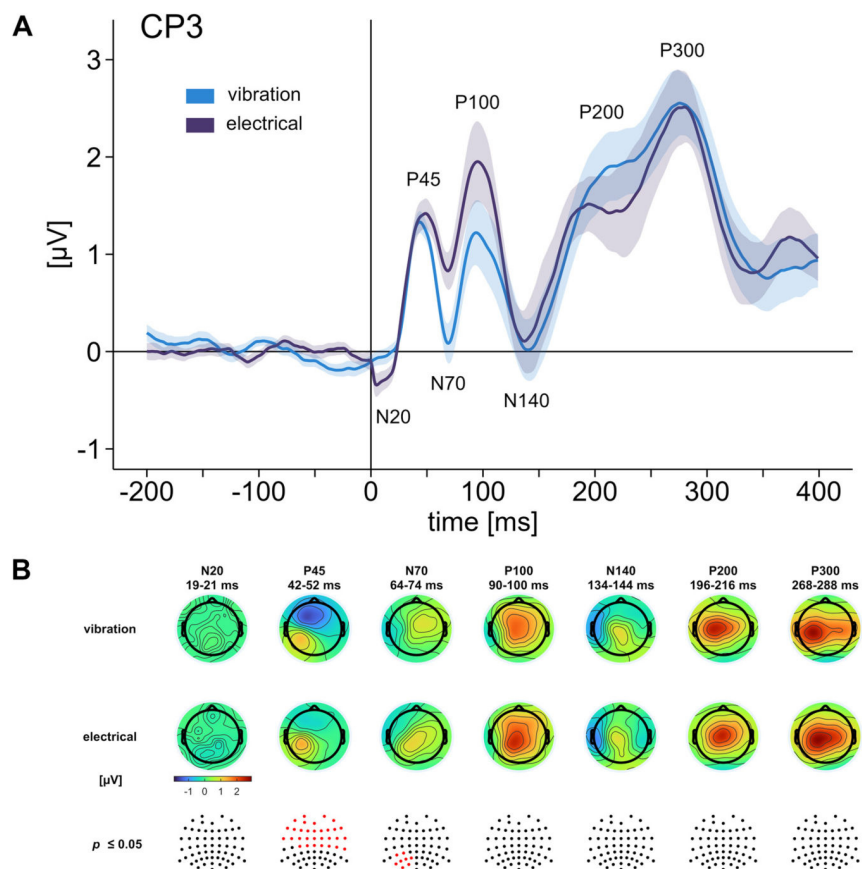
Figure 1. A: grand-averaged ($n = 32$) somatosensory evoked potential (SEP) waveforms following vibration at electrode CP3, showing P45, N70, P100, N140, P200, and P300 components. Error ribbons represent standard error. B: scalp topographies of grand-averaged ($n = 32$) activity for each vibration intensity at the P45, N70, P100, N140, P200, and P300 components.

stimulation intensity significantly increased P45 amplitude [Estimate = 0.0058, SE = 0.001, $t(92) = 4.97$, $P_{FDR} < 0.0001$], P100 amplitude [Estimate = 0.0066, SE = 0.001, $t(92) = 5.10$, $P_{FDR} < 0.0001$], P200 amplitude [Estimate = 0.0105, SE = 0.001, $t(92) = 7.11$, $P_{FDR} < 0.0001$], and P300 amplitude [Estimate = 0.0151, SE = 0.001, $t(92) = 9.77$, $P_{FDR} < 0.0001$]. Higher vibration intensity significantly decreased N140 amplitude [Estimate = -0.0024, SE = 0.001, $t(92) = -2.18$, $P_{FDR} = 0.038$], whereas no significant effect was found on N70 amplitude [Estimate = 0.0019, SE = 0.001, $t(92) = 1.64$, $P_{FDR} = 0.104$]. In summary, the uncorrected β estimates from the models predict amplitude increases of 0.058, 0.066, 0.105, and 0.151 μV for the P45, P100, P200, and P300 components, respectively, per 10 μm increase in vibration peak-to-peak-displacement. The decrease in the N140 amplitude predicted by the uncorrected β estimate from the model is -0.024 μV per 10 μm increase of vibration amplitude (see Supplemental Table S3 for full model details and Supplemental Fig. S1 for individual component

amplitude data). In the smaller subset of participants who received electrical stimulations, only the P100 showed a significant amplitude increase with stimulation intensity [Estimate = 1.4599, SE = 0.508, $t(59) = 2.88$, $P_{FDR} = 0.039$], corresponding to a predicted increase of 0.146 μV per 0.1 mA based on the uncorrected β estimate from the model. No significant effects of stimulation intensity were found for the N20, P45, N70, N140, P200, or P300 components. Full model results are reported in the Supplemental Table S4 and Supplemental Figs. S2 and S3.

In the subset of participants who received both vibrotactile and electrical stimulations, we computed averages across the four stimulation amplitudes for each stimulation type and channel. For both vibrations and electrical stimulation, we observed similar P45, N70, P100, N140, P200, and P300 components at CP3 (see Fig. 2A). In addition, there was an early negative deflection for the electrical stimulation corresponding to an N20 (see Fig. 2A). We computed the mean component amplitudes for the N20 (20 ± 1 ms), P45 (47 ± 5

Figure 2. A: grand-averaged ($n = 19$) activity for vibrotactile and electrical stimulation at CP3 show similar P45, N70, P100, N140, P200, and P300 components, with an additional N20 component observed only in electrical stimulation. Error ribbons represent standard error. B: scalp topographies of grand-averaged ($n = 19$) activity following vibrotactile and electrical stimulation for the N20, P45, N80, P100, N140, P200, and P300. Compared with electrical stimulation, vibrations produced a more pronounced negativity in frontal and central channels during the P45 time range and in contralateral centro-parietal channels during the N70 time range. Channels where vibrotactile and electrical stimulations differed significantly are highlighted in red. P values are corrected for testing multiple channels across components (30).



ms), N70 (69 ± 5 ms), P100 (95 ± 5 ms), N140 (139 ± 5 ms), P200 (206 ± 10 ms), and P300 (278 ± 10 ms). There was no significant difference in activation between the two stimulation types at any channel for the N20 [all $t(18) \leq 2.49$, $P_{FDR} \geq 0.188$, $d_z \leq 0.57$], P100 [all $t(18) \geq -2.3$, $P_{FDR} \geq 0.254$, $d_z \geq -0.53$], N140 [all $t(18) \leq 2.46$, $P_{FDR} \geq 0.198$, $d_z \leq 0.56$], P200 [all $t(18) \leq 1.88$, $P_{FDR} \geq 0.428$, $d_z \leq 0.43$], and P300 [all $t(18) \leq 2.12$, $P_{FDR} \geq 0.324$, $d_z \leq 0.49$] components (see Fig. 2B). Activation did however differ significantly between the two modalities for the P45 component at frontal and central electrodes Fp1/2, AF7/8, AF3, AFz, F7/8, F5/6, F3/4, F1/2, Fz, FT7/8, FC5/6, FC3/4, FC1/2, FCz, C1/2, C3/4, C6, Cz, and T8 [all $t(18) \leq -3.39$, $P_{FDR} \leq 0.036$, $d_z \leq -0.78$; see Fig. 2B]. In addition, activation differed significantly between vibrations and electrical stimulation for the N70 at contralateral parietal channels CP3, CP5, P1, P3, P5, P7, PO3 and PO7 [all $t(18) \leq -3.32$, $P_{FDR} \leq 0.041$, $d_z \leq -0.76$; see Fig. 2B].

To further examine the differences between vibrotactile and electrical stimulation seen in the P45 and N70, we used a source localization approach (see Table 1 for statistical results) on ROIs in the left hemisphere contralateral to the stimulation (see Fig. 3). During the P45 time window, vibrations compared with electrical stimulation resulted in significantly higher activation in the inferior frontal sulcus, the inferior and superior parts of the sulcus precentralis, the gyrus precentralis, the sulcus centralis, the

sulcus postcentralis, the gyrus postcentralis, the supramarginal gyrus, and in the transverse temporal sulcus (see Fig. 4 for source activation time courses). In contrast, there was significantly higher activation for electrical compared with vibrotactile stimulation in the intraparietal sulcus and transverse parietal sulci and in the posterior segment of the lateral fissure. In the time window of the N70, we found no significant differences between the two stimulation types in the superior frontal sulcus, the postcentral sulcus, the insula, or the superior temporal cortex.

DISCUSSION

To advance the use of naturalistic stimuli in somatosensory electrophysiology, we examined the SEPs of brief, Pacinian-targeted vibrations at varying amplitudes and compared them to those evoked by electrical stimulation. Unlike electrical stimulation, which nonselectively activates all four mechanoreceptor types and, depending on electrode placement, may also excite motor, proprioceptive, or nociceptive fibers, high-frequency vibrations selectively engage the Pacini mechanoreceptor. In addition, vibrotactile stimulation is better suited to study real-world touch and special populations, such as patients, children, or older adults, as it is experienced as less aversive than electrical stimulation.

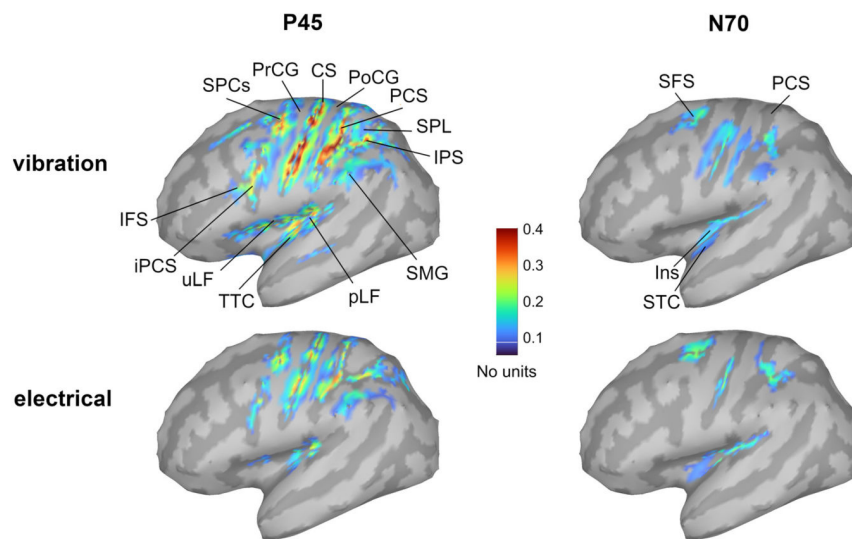


Figure 3. Grand-average ($n = 19$) source estimates for the P45 (42–52 ms) and N70 (64–74 ms) components, shown for vibrations (top) and electrical stimulation (bottom) in the left hemisphere. IFS, inferior frontal sulcus; CS, central sulcus; iPCS, inferior part of the precentral sulcus; sPCS, superior part of the precentral sulcus; PrCG, precentral gyrus; PoCG, postcentral gyrus; TTC, transverse temporal cortex; IPS, intraparietal sulcus; SMG, supramarginal gyrus; SPL, superior parietal lobule; uLF, upper bank of the lateral fissure; pLF, posterior segment of the lateral fissure; PCS, postcentral sulcus; SFS, superior frontal sulcus; Ins, insula; STC, superior temporal cortex. Colors represent dSPM-normalized activity (arbitrary units).

Both stimulation modalities produced centro-parietal SEPs of similar morphology, namely a P45, N70, P100, N140, P200, and P300. These are commonly observed SEPs reported following electrical median nerve stimulation at the wrist (43), electrical stimulation at the fingers (44–47), air puffs (6, 47, 48), and single taps (49–51). The earlier N20, associated with the arrival of thalamic information in SI (52), was visible following electrical stimulations. As reported in prior studies (6, 18), this is likely due to the less synchronous activation of Pacinian receptors compared with the direct excitation of the median nerve with electrical stimulation. Such asynchronous activity from mechanical stimulation may generate a weaker signal that is more difficult to detect at the scalp, although the N20 has previously been reported for air puffs (47, 53). Thus, it is notable that despite the enhanced signal-to-noise ratio achieved through a high number of repetitions, no short-latency component prior to 45 ms was visible even for brief vibrations. The first short-latency component elicited by vibration is the P45, which is influenced by the physical characteristics of the somatosensory stimulus (54), consistent with the stimulation intensity scaling observed here. It primarily originates from areas 3b and 1 in contralateral SI (18, 55) with possible SII involvement indicated by magnetoencephalography (56). Other studies using vibrations from 10 to 240 Hz (18, 57, 58) report the P45 as well, whereas some studies do not (17, 59, 60), suggesting protocol-dependent effects. The subsequent N70 reflects processing in contralateral SI (43, 61) and SII (40, 43, 62). The P100 originates in bilateral SII (43) and, similar to the earlier components, is modulated by stimulus characteristics (54). The N140 has frontal contributions (43) and marks the earliest correlate of conscious perception (54). Likewise, the P200 and P300 are associated with later processing and reporting of tactile stimuli (54). Altogether, suprathreshold high-frequency vibrations are well suited to generate both short-latency cortical SEPs as well as longer latency components.

Both short- and long-latency components scaled with vibration amplitude, with the exception of the N70. We replicated the known amplitude scaling for Pacini-level vibrations at the P200 and P300 components (17). We also observed a scaling effect with vibration amplitude even earlier for the P45, P100, and N140, and report the expected voltage change in the SEP per unit increase in vibration peak-to-peak amplitude. Our findings complement reports of intensity-dependent scaling of short-latency SEPs (<50 ms) in other modalities, including electrical stimulation of the median nerve (15, 54, 63) or the finger (45), and air puff stimulation (6, 64). Intensity modulation for longer-latency components (P100, N140, P300) has also been documented for electrical stimulation (14). We did not observe significant intensity scaling in the N70 reported with air puffs (64–66) and electrical finger stimulation (54), indicating statistical power may have been too low to detect such an effect. Importantly, we only assessed intensity modulation under suprathreshold stimulation. Although our modeling approach included intercepts for theoretical SEP size at zero stimulation, these should not be interpreted since the relationship between SEP and vibration amplitudes at lower intensities is likely nonlinear and warrants further investigation. Furthermore, we did not directly compare amplitudes between vibration and electrical stimuli. Electrical stimulation intensities were matched perceptually to vibrations, rather than tailored to individual thresholds (e.g., thumb twitch), and held constant across participants. This strategy provided a standardized reference for expected SEP magnitudes in a healthy young population (see Supplemental Material). The perceptual matching approach resulted in four electrical intensities that were not evenly spaced. Moreover, although vibrotactile stimuli of all four intensities were randomized within each block, electrical stimuli, though also randomized within blocks, had to be split into two separate blocks for low and high intensities due to manual adjustment requirements of the stimulation device. Notably, the intensity difference was greater between the two lower amplitudes than between the two higher amplitudes. Thus, since electrical SEPs may

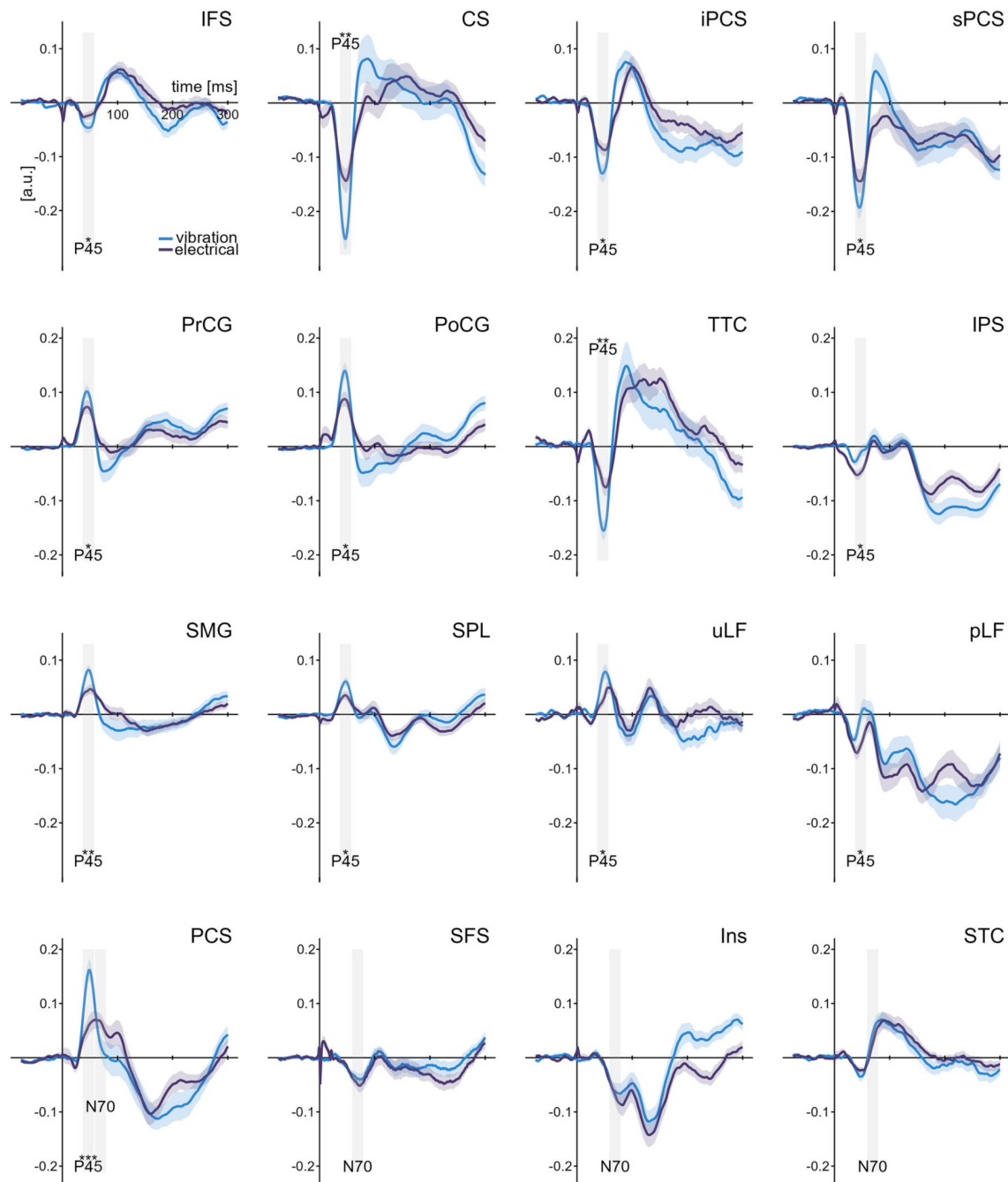


Figure 4. Time series of the grand-averaged ($n = 19$) activation following vibrotactile and electrical stimulation within the selected regions of interest (ROIs). The y-axis represents dSPM-normalized activity (arbitrary units). IFS, inferior frontal sulcus; CS, central sulcus; iPCS, inferior part of the precentral sulcus; sPCS, superior part of the precentral sulcus; PrCG, precentral gyrus; PoCG, postcentral gyrus; TTC, transverse temporal cortex; IPS, intraparietal sulcus; SMG, supramarginal gyrus; SPL, superior parietal lobule; uLF, upper bank of the lateral fissure; pLF, posterior segment of the lateral fissure; PCS, postcentral sulcus; SFS, superior frontal sulcus; Ins, insula; STC, superior temporal cortex. Error ribbons represent standard error. Shaded gray areas indicate the P45 and N70 time windows within which vibrotactile vs. electrical stimulation comparisons were performed; statistical results from t tests and Wilcoxon signed-rank tests for these windows are reported in Table 1. *** $P_{FDR} < 0.001$, ** $P_{FDR} < 0.01$, * $P_{FDR} < 0.05$.

reflect both the absolute intensity of stimulation and the relative intensity differences within each block we did not compare intensity modulation across the two modalities. Together, our results demonstrate that vibration intensity is robustly represented in early cortical processing and clearly reflected in SEP amplitudes. Although this representation may have been more subtle during early stages of sensory integration, it re-emerged during later stages of somatosensory integration (P100 and later).

In addition, we contrasted vibrotactile and electrical SEPs (see Fig. 2B). The long-latency components (P100, N140, P200, and P300) exhibited comparable topographies across stimulation types, suggesting engagement of similar somatosensory networks after initial processing. These components were characterized by a broadly central scalp distribution, with the P300 showing a bilateral central positivity and the N140 showing a contralateral temporal negativity. In contrast, the short-latency P45 component following vibrations showed a pronounced frontal negativity absent during electrical stimulation, suggesting distinct cortical generators despite comparable SEP morphology at electrode CP3. Importantly, although intensities were randomized within each block, electrical stimulation blocks included only two intensities, whereas vibration blocks included four. Consequently, electrical stimulation was overall more predictable than vibration. For comparisons between stimulation types, we averaged across intensities to mitigate this imbalance. Nevertheless, the higher predictability of electrical stimulation remains a limitation and may have influenced SEP amplitudes through differential expectations or attentional effects.

Source analysis indicated stronger contralateral activation in precentral regions and SI for vibrations. Posterior parietal activation patterns showed a differential pattern: vibrations engaged the superior parietal lobule and supramarginal gyrus more strongly, i.e., regions involved in sensorimotor (67) and multisensory (68, 69) integration. Conversely, electrical stimulation preferentially activated intraparietal and transverse sulci, i.e., regions related to multisensory processing (70, 71). Differential activation was also observed in regions along the lateral fissure and parietal operculum, corresponding to SII (40, 72, 73), with vibrations predominantly activating anterior areas and electrical stimulation more posterior regions. These findings align with parallel early engagement of SI and SII (56, 74) and may reflect distinct processing of the two stimulation modalities within SII, consistent with reports of stimulus-dependent responses in SII (75–79). Similar to the P45, the N70 component differed in scalp topography, showing lower activity in contralateral parietal channels for vibrotactile than for electrical stimulation. However, we found no differences in source activation during the N70 time window, indicating similar neural sources at later processing stages. Taken together, these findings suggest that vibration and electrical stimulation engaged different cortical sources during early somatosensory processing and integration. At later stages, they appear to converge on shared neural resources, as reflected in similar source activation during the N70 time window and the shared topography of long-latency SEPs. The differences likely stem from the selective excitation of RAI fibers by high-frequency vibrations as opposed to the activation of all four sensory

fiber subtypes by electrical stimulation. In sum, while the absence of individual head anatomies limits precise source localization, our findings suggest possible differences in early-stage cortical processing dynamics between vibrotactile and electrical stimulation. These results could motivate future investigations using more spatially precise methods such as functional magnetic resonance imaging.

Our source activation results contrast with prior studies showing stronger SI activity for electrical median nerve stimulation (80) and electrical stimulation at the fingers (47) compared with air puffs for somatosensory evoked magnetic fields (SEFs) in the 40–50 ms time range. A key limitation in those studies is the lack of perceptual intensity matching between modalities, which may have inflated the apparent effect of electrical stimulation. Indeed, Rossini et al. (47) observed lower SEF amplitudes for mechanical compared with electrical stimulation. In our study, by matching perceived intensity between vibration and electrical stimulation (see Supplemental Material), we ensured a fairer comparison. Although P45 amplitude scaled with vibration intensity, the similar P45 amplitude across both stimulation types at CP3 suggests this matching was effective. Another critical aspect is that both electrical and mechanical stimulation at the index finger only activate sensory fibers, whereas traditional median nerve stimulation at the wrist additionally orthodromically excites motor and possibly proprioceptive fibers, which may explain the higher source activation for electrical median nerve stimulation found in the study by Forss et al. (80). Moreover, these studies measured SEFs, which predominantly originate from tangential sources, whereas our analysis of SEPs using constrained dipoles favored radial sources (81). Thus, given the matched intensities and the unlikely contribution of motor fibers, we argue that the differences here are purely sensory due to receptor-specific activation. A more recent SEP study (57) did not find significant source activation differences at P45 for 250 Hz vibrotactile versus electrical stimulation but indicated reduced SI activation at N70 for vibrations. Although these findings diverge from ours, they highlight the need for further research into early cortical dynamics of different somatosensory stimulation modalities, using more precise spatial localization techniques.

In sum, we provide a comprehensive overview of short- and long-latency SEPs evoked by Pacinian-targeted vibration, detailing contralateral CP3 waveforms and associated scalp topographies. We showed clear intensity scaling of the P45, P100, N140, P200, and P300 components with vibration amplitude. By detailing how SEP components are expected to scale with stimulus amplitude, our findings offer a reference for future studies. Moreover, selective Pacinian activation, compared with intensity-matched electrical stimulation, elicited stronger early cortical responses in contralateral SI and differentially activated posterior parietal areas and SII. At later integrative and cognitive stages, we observed no divergence in neural circuits across stimulation types. Together, these results improve the ecological validity of SEP paradigms by using vibrotactile stimulation for investigating somatosensory processing more closely related to real-world touch.

DATA AVAILABILITY

Anonymized data have been deposited in Open Science Framework (<https://doi.org/10.17605/OSF.IO/EJ73Z>).

SUPPLEMENTAL MATERIAL

Supplemental Tables S1–S4 and Supplemental Figs. S1–S3: <https://doi.org/10.17605/OSF.IO/34QT8>.

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

E.F. and K.F. conceived and designed research; E.F. performed experiments; E.F. analyzed data; E.F., L.K.M., and K.F. interpreted results of experiments; E.F. prepared figures; E.F. drafted manuscript; E.F., L.K.M., and K.F. edited and revised manuscript; E.F., L.K.M., and K.F. approved final version of manuscript.

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4 Study III: Temporal dynamics of early somatosensory processing in goal-directed actions

Temporal dynamics of early somatosensory processing in goal-directed actions

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Abstract

Tactile sensitivity is temporally modulated on a moving limb. Yet the neural mechanisms underlying this modulation remain unclear. Using electroencephalography, we examined the temporal dynamics of early somatosensory processing during goal-directed reaching.

Participants reached for their unseen left hand while brief vibrations were applied to the moving right index finger in different movement phases. Psychophysical results revealed overall tactile suppression during reaching, with sensitivity transiently improving around maximum speed relative to the late movement phase. Consistent with the psychophysical data, the short-latency P45 component, originating in primary somatosensory cortex, was suppressed during reaching but recovered around maximum speed. Reduced P45 amplitudes were associated with stronger tactile suppression measured behaviorally, linking early cortical activity to perceptual changes. This temporally specific modulation of tactile perception, associated with early cortical processing, suggests that the somatosensory system dynamically adapts its sensitivity to facilitate sensorimotor control in goal-directed actions.

Significance statement

The perception of touch on a moving hand varies across different movement phases, depending on the importance of sensory feedback for guiding the hand. Our results show that these changes in perception are linked to modulations in early brain activity, indicating that the central nervous system adjusts touch processing in a time-sensitive manner at early processing stages to facilitate control of goal-directed actions.

Introduction

Goal-directed movements depend on somatosensory signals. For example, tactile sensations directly arise from physical interactions involving the moving limb, and proprioceptive and tactile feedback inform about limb position and movement dynamics. Some of these somatosensory signals provide essential information for sensorimotor control (Goulding et al., 2025), whereas others may be irrelevant. Because feedback-based mechanisms alone are inherently noisy (Faisal et al., 2008) and temporally delayed (Miall & Wolpert, 1996), the sensorimotor system likely integrates sensory feedback with predictive feedforward models using efference copies of motor commands to estimate future sensory states of the moving limb (Desmurget & Grafton, 2000).

A well-documented perceptual phenomenon related to sensorimotor control is a reduction in tactile sensitivity on the moving limb, known as tactile suppression (Chapman et al., 1987). This phenomenon has been demonstrated by behavioral studies across a wide range of actions and is complemented by electroencephalographic (EEG) findings, showing reduced amplitudes of somatosensory evoked potentials (SEPs) during movement, particularly at short-latency components like the N20 and P45 (Lei et al., 2018; Rossini et al., 1999; Rushton et al., 1981), associated with early-stage processing in primary somatosensory cortex (S1) (Allison et al., 1992).

Crucially, tactile suppression is not an all-or-nothing phenomenon: When sensory input from the moving limb is relevant to successfully perform the movement, tactile sensitivity is preserved to some extent, although partial suppression may persist. For example, tactile suppression is less pronounced on the index finger when grasping an object with a precision grip, as opposed to other parts of the hand and arm (Colino et al., 2014; Manzone et al., 2018), or when grasping a slippery versus a high-friction object without seeing it (Voudouris & Fiehler, 2022). Tactile perception also recovers on the lower leg shortly before dealing with

perturbations during a balancing task (Wachsmann et al., 2025b). Likewise, tactile suppression is evident during targeted reaching movements without visual feedback, which rely exclusively on somatosensory inputs (Voudouris & Fiehler, 2021). Importantly, tactile suppression during such reaching actions follows distinct temporal dynamics, as it is transiently released around the time of maximum speed (Voudouris & Fiehler, 2021), i.e., the onset of the deceleration phase when sensory guidance of the movement becomes particularly important (Elliott et al., 2001). Together, these findings demonstrate a flexible modulation of tactile suppression according to the functional relevance of somatosensory feedback. However, because these observations are based on behavioral measures only, it remains unclear whether changes in tactile perception reflect corresponding neural modulations in early somatosensory processing.

Electrophysiological studies provide some evidence for relevance-based modulation of SEPs from the moving limb: short-latency SEP amplitudes increase during exploratory hand movements compared to rest (Knecht et al., 1993), and during lower limb movements in a balancing task when an upcoming perturbation challenges posture (McIlroy et al., 2003). In a magnetoencephalographic study, the somatosensory evoked field component M38 was enhanced during grasping movements relative to rest and further increased during a more complex ball rotation task (Wasaka et al., 2017). While these electrophysiological studies did not measure psychophysical aspects of tactile perception, they suggest that facilitation of early somatosensory processing may underlie the modulation of tactile suppression during movement as sensory relevance changes.

To jointly examine the behavioral and neural correlates of this dynamic modulation, we combined psychophysics with EEG recordings of SEPs during a reaching task previously shown to modulate tactile perception (Voudouris & Fiehler, 2021). First, we asked whether tactile sensitivity is modulated across different movement phases; second, whether early cortical processing indexed by the P45 component shows a corresponding temporal modulation; and

third, whether temporal changes in tactile sensitivity are linked to changes in cortical processing. Based on prior evidence (Rossini et al., 1999; Rushton et al., 1981), we predicted that movement-related tactile suppression would correspond to reductions in the early P45 component and that the time course of P45 amplitudes would mirror the temporal dynamics of suppression across movement phases.

Materials and Methods

Experimental Design

Vibrations (20 ms, 280 Hz) were delivered using a vibrotactile stimulation device (PiezoTac tactor; Engineering Acoustics Inc., Casselberry, FL, USA). The tactor comprised a skin contactor (6.4 mm diameter) mounted on a shielded cantilever. Cantilever vibrations produced sinusoidal oscillations perpendicular to the skin. One contactor was placed on the palmar side of the proximal phalanx of the right index finger, leaving the fingertip uncovered. A second contactor was positioned on the sternum, approximately 3 cm below the clavicle. The contactors were fixed to the participant's skin using medical tape. The experiment was controlled by custom MATLAB (The MathWorks Inc., Natick, MA, USA) software using the Psychtoolbox extension (Brainard, 1997). The position of an infrared marker on the nail of the right index finger was recorded at 250 Hz with an Optotrak Certus motion tracking system (Northern Digital Inc., Waterloo, ON, Canada).

Procedure

Participants placed both hands on a table in front of them. The left hand rested palm-down with the thumb and index finger on specific markers positioned 10 cm to the left of the body midline, to ensure consistent placement. The right hand rested on a keypad located 18 cm to the right of the midline and 20 cm in front of the participant. Throughout the experiment, participants' view of their hands was occluded using a tilted cardboard screen, which allowed them to see the top of the computer monitor for instructions. At the beginning of each trial, participants held down

a key with their right index finger to initiate the trial. Text on the computer screen then indicated the target finger on the left hand (thumb or index), and participants had 2500 ms to initiate the movement. Upon releasing the key, participants performed a reaching movement with the right hand to touch the nail of the specified target finger. A standard vibration (peak-to-peak displacement: 119 μm) was delivered to the moving right index finger at one of five possible latencies relative to movement onset (50, 150, 250, 350, or 450 ms), which was determined by the key release. After reaching the target, participants rested their right hand next to the left hand on the table. A comparison vibration was delivered to the sternum 3000 ms after the standard vibration, well after movement completion, while both hands were still. The comparison stimulus had one of seven possible intensities (peak-to-peak displacement: 47, 71, 95, 119, 143, 167, or 192 μm). Participants indicated which of the two vibrations felt more intense by pressing foot pedals: the left pedal for the first vibration (on the hand) and the right pedal for the second vibration (on the sternum; see Fig. 1 for the trial sequence). Each stimulation time was presented 70 times for a total of 350 trials. Additionally, 70 trials (16.67% of all trials) were included to record movement-related EEG without vibrotactile stimulation, matching the number of trials for each stimulation time. In these omission trials, participants were informed that no vibration was given 3000 ms after movement onset and no tactile discrimination response was required. Participants completed 10 blocks of 42 trials each. Within each block, all combinations of stimulation time and comparison intensity were presented once, along with seven omission trials in random order. Trials were repeated at the end of the block if participants initiated the movement too early, less than 180 ms after target presentation, suggesting the cue had not been processed, or if they failed to initiate movement within 2500 ms after the cue. Self-paced breaks were provided between blocks. Before starting the experiment, participants familiarized themselves with the reaching movement and the discrimination task in 20–40 practice trials. We also assessed tactile sensitivity at rest by asking

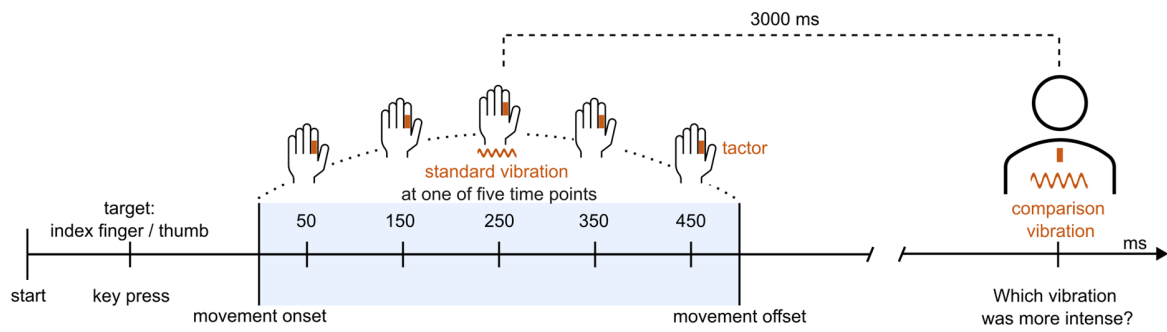


Fig. 1: Trial Sequence.

Participants initiated each trial by pressing and holding a key with the right index finger. Text on the monitor indicated the target finger of the left hand. Participants released the key and reached toward the target finger of the left hand. A standard vibration of fixed amplitude was delivered to the right index finger at one of five time points during the movement (250 ms shown here). After an ISI of 3000 ms, a comparison vibration of varying amplitude was presented on the sternum. Participants judged which vibration felt stronger using foot pedals. Participants also performed the same psychophysical task with both hands at rest.

participants to perform the discrimination task without movement, while both hands remained on the table in the same position adopted after the reaching movements. This enabled us to assess relative changes between rest and movement phases and determine the effect of movement on tactile processing while accounting for idiosyncrasies in tactile sensitivity. The standard vibration was presented to the right index finger at one of five delays (50, 150, 250, 350, or 450 ms) after a fixed interval of 700 ms from trial onset, replicating the relative timing used during movement. A comparison vibration followed on the sternum 3000 ms later. Participants judged vibration intensity using foot pedals. Each of the seven comparison intensities was presented twice per stimulation time (70 trials total). Trials ended only after participants had responded and at least 6000 ms had elapsed from trial onset, ensuring a trial duration consistent with the reaching block. Trials started automatically after a foot pedal was pressed. The rest condition was divided into two blocks, separated by a short break, and both blocks were administered either before or after the movement blocks, counterbalanced across participants.

Participants

Thirty-eight participants (self-reported gender: 22 female, 16 male; mean age: 25.7 years, SD = 4.1) provided written informed consent and received either course credit or 10 €/hour as compensation. The study was approved by the ethics committee of the Justus Liebig University Giessen and conducted in accordance with the Declaration of Helsinki (World Medical Association, 2013), with the exception of pre-registration. All participants were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971) ($M = 90.8$, range = 28.6–100). Two participants were excluded for slow movements, leaving too few stimulus presentations in the late post-max speed phase to fit psychometric functions (see Kinematic Analysis); one participant was excluded because 86% of trials were rejected (see Kinematic Analysis); one participant was excluded as a statistical outlier (see Statistical Analysis).

Kinematic Analysis

The kinematic data were analyzed in MATLAB (R2021a; The MathWorks Inc., Natick, MA). Movement speed was computed by numerical differentiation of the three-dimensional data divided by the sampling interval of 4 ms. Movement onset was defined as the key release. Mean reaction time was 547 ± 240 ms (standard deviation across participants). Movement offset, i.e., when participants touched the target finger, was determined using the multiple sources of information method to form a composite score (Schot et al., 2010): Coarse spatial constraints excluded frames with lateral positions near the start zone (all positions within 20 cm to the left and 10 cm to the right of the start position were excluded). To lower the likelihood of frames after touching the target finger, frames were down-weighted when the moving index finger was within 3 cm of the location on the table where participants rested their hand after the touch. A timing gate increased the likelihood of a frame being the end of the movement once speed fell below 0.10 m/s after the speed maximum (identified within 400 ms following movement onset) and maintained this elevated score for 80 ms. Lower instantaneous speed, smaller x (toward the

target hand), and larger y (further from the body) also increased the score. The movement end was defined as the frame with the highest composite score likelihood.

Movement duration ($M = 562$ ms, $SD = 100$ ms) was defined as the time between movement onset and offset. Time of maximum movement speed was determined for each trial. To account for inter-individual differences in movement duration, the timing of maximum speed was normalized to the total movement duration in each trial. Across participants, the average maximum speed was 1.22 ± 0.19 m/s, occurred after 202 ± 62 ms and at $33 \pm 6\%$ of the movement. Because maximum speed denotes the onset of the period when sensory guidance of the hand toward the target gains importance (Elliott et al., 2001), stimulation trials were assigned to four movement phases defined relative to maximum speed: (1) pre-max speed (2) window of $\pm 5\%$ around max speed (3) early post-max speed, the first 40% of the remaining post-max duration; and (4) late post-max speed, the final 60% of the remaining post-max duration. These time bins will be referred to as the four movement phases. We used a 40/60 rather than 50/50 proportion to divide the post-max time to balance trial counts: The average movement duration was 562 ms, while the latest stimulation occurred 450 ms after movement onset, which resulted in too few late-phase trials for stable psychometric fits under a 50/50 post max speed split in eight participants. The 40/60 proportion allowed for stable psychometric fits in seven of these eight participants. Critically, the 40/60 split also yielded more balanced trial counts per movement phase, with phases 1–4 containing on average 32.9%, 13.7%, 27.1%, and 26.3% of trials, respectively. We allowed fewer trials in the small window around maximum speed to maintain temporal specificity in this movement phase.

Trials were excluded from all further analyses if the movement end could not be determined (empty composite score; $< 1\%$ of trials), if $>25\%$ of motion-tracking samples were missing in the last third of the movement due to marker occlusion (1% of trials), if the mean speed during the first 20% of the movement was below 10 m/s (1% of trials), indicating delayed movement

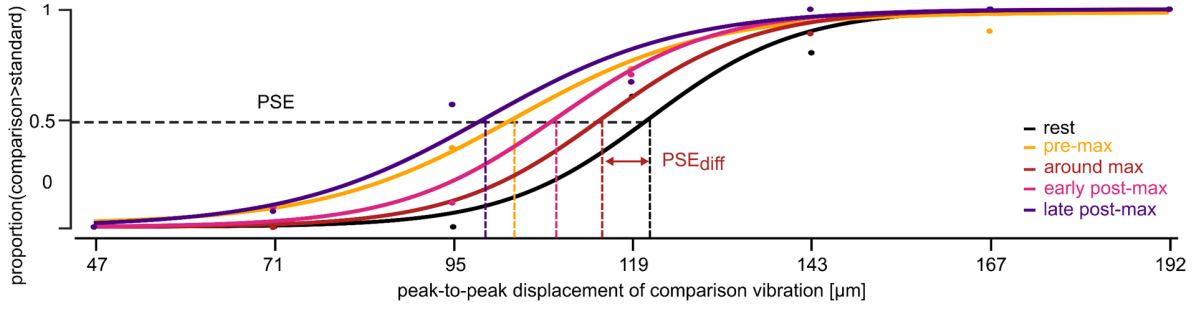


Fig. 2: Psychometric curves of one example participant.

Psychometric curves were fitted to the participant's responses in the comparison task, both for the rest condition and for each movement phase. The PSE was determined as the 50% point of each curve. To control for individual differences in tactile sensitivity, the PSE from each movement phase was subtracted from the PSE in the rest condition, yielding one difference score per movement phase (PSE_{diff}).

initiation after start key release and incorrectly timed tactile stimulations, if the movement duration was >3 SD above the participant's within-block mean (1% of trials), or if the stimulation occurred after the movement had ended (4% of trials).

Psychophysics Analysis

Logistic psychometric functions were fitted to participants' responses in the psychophysical task using the maximum likelihood estimation implemented in the Psignifit 4 toolbox (Schütt et al., 2016) in MATLAB. Separate functions were fitted for each participant, both for the four movement phases and for the resting condition. Across participants, the mean number of trials included in the rest condition, pre-max, around max, early post-max, and late post-max phases was 70, 108, 45, 88, and 83, respectively. PSEs were derived from the 50% point of each function. To control for inter-individual differences in tactile intensity discrimination, the PSE in each of the four movement phases was subtracted from the corresponding values in the rest condition to compute four normalized difference scores (PSE_{diff}) per participant (see Fig. 2).

EEG Analysis

EEG data were recorded from 37 channels (Fp1, C3, P3, P4, C4, AF7, AF3, AFz, F1, F5, FT7, FC3, C1, C5, TP7, CP3, P1, P5, PO7, PO3, POz, PO4, PO8, P6, P2, CPz, CP4, TP8, C6, C2, FC4, FT8, F6, AF8, AF4, F2, FCz) placed according to the international 10–20 system, using a BrainProducts actiCap with a 64-channel LiveAmp system and BrainVision Recorder software (Brain Products GmbH, Gilching, Germany), sampled at 500 Hz. In addition, electrodes were placed at the outer canthi of both eyes and below the left eye to record horizontal and vertical eye movements. Data were processed using eeglab 2024.2 (Delorme & Makeig, 2004) in MATLAB. Preprocessing involved high-pass filtering (non-causal Butterworth impulse response, half-amplitude cut-off at 0.1 Hz, 12 dB/octave roll-off), removal of DC offsets, and attenuation of 50 Hz line noise using Zapline-plus (Klug & Kloosterman, 2022). Data were re-referenced offline to the average of the linked earlobes. Noisy channels were identified through visual inspection and interpolated. Independent component analysis (ICA) was performed using the Infomax algorithm, with PCA rank reduction used when channels had been interpolated. Ocular artifacts were removed by ICA and ICLabel classification (Pion-Tonachini et al., 2019). Remaining artifacts were rejected via artifact subspace reconstruction. Stimulation triggers were latency-corrected by 4 ms as determined in a dedicated test run of the experiment using a StimTrak system (BrainProducts, Germany) with an audio adapter and a contact microphone attached to the stimulator's skin contactor. Data were low-pass filtered using a non-causal Butterworth filter (40 Hz half-amplitude cut-off, 12 dB/octave roll-off). EEG data were segmented into epochs from -460 to 400 ms relative to the vibration onset at the possible five stimulation time points (50, 150, 250, 350, and 450 ms post movement onset) and baseline-corrected using the 200 ms pre-stimulus interval. For omission trials, epochs were extracted in the same manner around the five time points (50, 150, 250, 350, and 450 ms post movement onset), to obtain the EEG activity associated with movement at the corresponding vibration delivery times.

These omission epochs were averaged separately for each time point and subsequently subtracted from the respective stimulation epochs, isolating the SEPs (see Fig. 3A). The resulting difference waves were grouped into four movement phases by stimulation timing relative to each trial's maximum speed (pre-max, around max, early post-max, late post-max; see Kinematic Analysis) and averaged within each phase (see Fig. 3B). Mean trials per participant were 64, 96, 41, 80, and 78 in the rest condition, pre-max speed, around max speed, early post-max speed, and late post-max speed phases, respectively. On average, 61 omission trials were analyzed per person and time point. The analysis focused on electrode CP3 over S1 contralateral to the stimulated right hand. Components were identified individually from each participant's within-subject average trace across the rest condition and the four movement phases (see Fig. S1). Within predefined ranges, positive peaks were located for the P45 (35–55 ms) and P300 (250–350 ms). Measurement windows were set at ± 5 ms of peak latency for P45 and ± 10 ms for P300. Mean amplitudes were then extracted per participant, rest condition and movement phase within these windows. Next, we computed differences scores by subtracting the mean component amplitude of each of the four movement phases from the mean component amplitude of the rest condition, resulting in one $P45_{\text{diff}}$ and $P300_{\text{diff}}$ score per movement phase. This rest-movement subtraction was chosen to maintain consistency with the computation of the psychophysical measure.

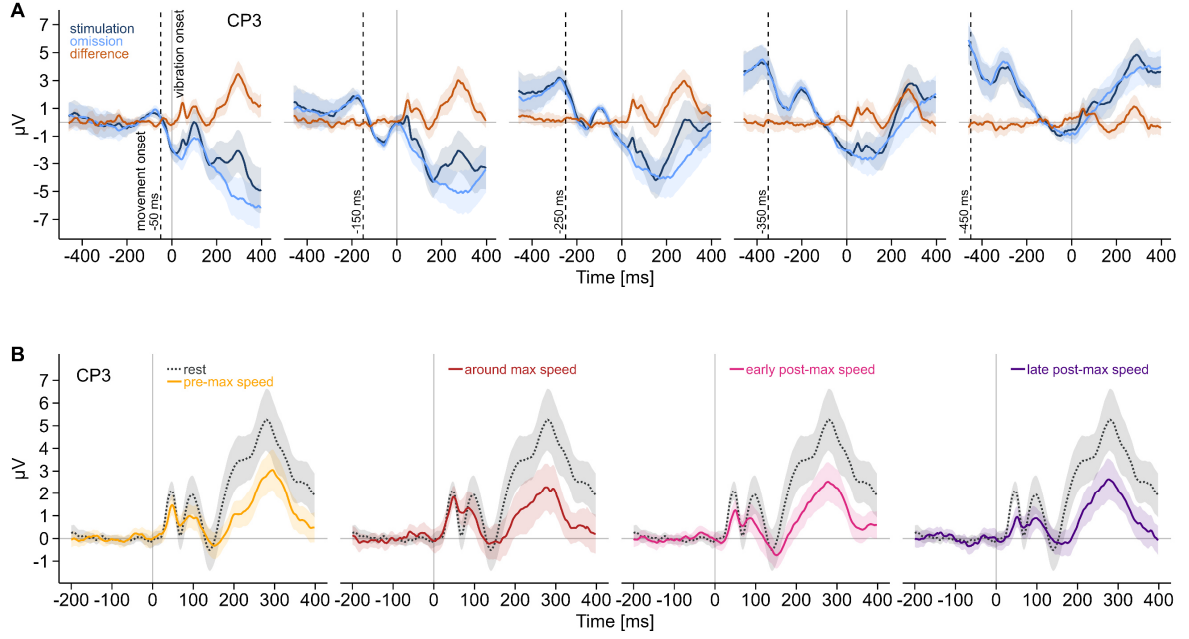


Fig. 3: Grand-averaged EEG activity and difference waves across movement phases.

A. Grand-averaged EEG responses ($n = 34$) for stimulation and omission trials. Stimulation trials with movement and vibrations delivered at five time points (50, 150, 250, 350, 450 ms) post movement onset. EEG was epoched to vibration onset and baseline corrected to the 200 ms pre-stimulation interval. Omission trials with movement only, epoched at the same five time points (50, 150, 250, 350, 450 ms) post movement onset and baseline corrected to the preceding 200 ms. Difference waves computed as stimulation minus omission to isolate SEPs. The dotted vertical line shows movement onset. Omission traces in all subpanels are the same data re-epoched; stimulation traces differ by stimulation time. Shaded bands show 95% CIs. **B.** Grand-averaged difference-wave SEPs ($n = 34$) grouped into four phases relative to maximum movement speed: pre-max speed (yellow), around max speed (red), early post-max speed (pink), late post-max speed (purple). Rest condition SEPs, shown for reference (black dotted), are the same in each subpanel. Shaded bands show 95% CIs.

Statistical Analysis

To assess whether movement suppressed vibration perception, we compared the PSE_{diff} from each of the four movement phases with zero using paired, two-sided t -tests. Modulation of tactile perception across the movement time course was tested with a univariate repeated-measures ANOVA on the PSE_{diff} from the four movement phases. Post hoc comparisons used paired-samples t -tests between movement phases.

To examine modulations in the SEPs associated with movement, we tested $P45_{diff}$ and $P300_{diff}$ from each movement phase against zero using paired, two-sided t -tests. To assess a modulation

of component amplitudes across the four movement phases, univariate repeated-measures ANOVAs were performed on $P45_{\text{diff}}$ and $P300_{\text{diff}}$ separately, followed by paired post-hoc t-tests between movement phases. Planned contrasts that were motivated by significant differences in PSE_{diff} were one-sided; all other comparisons were two-sided. The covariation of perception with changes in SEPs was tested using Pearson correlation. To assess whether SEP amplitudes varied with changes in tactile perception, Pearson correlations were computed between SEP differences and corresponding PSE_{diff} values across phases.

The false discovery rate was controlled within each test family using the Benjamini-Hochberg method, and adjusted p -values are reported (Benjamini & Hochberg, 1995). Effect sizes are reported as Cohen's d_z and partial η^2 (Lakens, 2013). Data were analyzed in R, v.4.3.3 (R Core Team, 2024) with a significance level of $\alpha = 0.05$. Greenhouse-Geisser correction was applied when sphericity was violated (Mauchly's test). Univariate outliers were defined as $|z| > 3$ based on means and standard deviation within movement phases. Bivariate outliers were defined by Mahalanobis distance (D^2) with a cutoff of $\chi^2(2, 0.999) = 13.82$ (Finch, 2012; Hardin & Rocke, 2005). One participant was classified as both a univariate outlier ($z = -3.63$) within $P45_{\text{diff}}$ in the around max speed phase and as a bivariate outlier for $P45_{\text{diff}}$ and PSE_{diff} ($D^2 = 23.09$). Data from this participant were excluded from the primary analyses (see Supplement and Fig. S2 for the analysis without this outlier exclusion).

Results

To account for individual differences in tactile processing, movement-related changes were expressed as difference scores, obtained by subtracting PSEs and P45 amplitudes obtained during movement from those measured at rest (PSE_{diff} and $P45_{\text{diff}}$; see Methods). Positive PSE_{diff} and $P45_{\text{diff}}$ values reflect reduced tactile sensitivity and smaller SEP amplitudes, respectively, during movement relative to rest.

To test tactile suppression during movement, we compared PSE_{diff} from each movement phase to zero using paired t-tests. Tactile sensitivity was suppressed relative to rest, with PSE_{diff} significantly greater than zero in all phases of the movement: pre-max speed ($t(33) = 3.47, p = 0.002, d_z = 0.59, 95\% \text{ CI } [5.54-21.24]$), around max speed ($t(33) = 2.48, p = 0.019, d_z = 0.42, 95\% \text{ CI } [1.73-17.59]$), early post-max speed ($t(33) = 3.59, p = 0.002, d_z = 0.62, \text{ CI } = [6.36-23.01]$), and late post-max speed ($t(33) = 4.20, p < 0.001, d_z = 0.72, 95\% \text{ CI } [9.23-26.60]$). A repeated-measures ANOVA used to assess the temporal dynamics of suppression revealed a main effect of movement phase ($F(3, 99) = 4.66, p = 0.004, \eta^2_p = 0.12$). Post-hoc comparisons showed weaker suppression (i.e., improved sensitivity) around max speed than in the late post-max phase ($t(33) = -3.3, p = 0.014, d_z = -0.57, 95\% \text{ CI } [-13.35- -3.16]$), in line with previous findings (Voudouris & Fiehler, 2021). Suppression did not differ significantly between the other movement phases (all $t(33) \geq -2.5, p \geq 0.053, d_z \geq -0.43$; see Fig. 4A).

We focused the EEG analysis on electrode CP3 located over S1 contralateral to the stimulated right hand, since P45 amplitude is maximal at this site (Yamada, 2014). Figure 2A shows the waveforms, and Figure 2B the respective scalp maps. To assess SEP gating during movement, we tested $P45_{diff}$ against zero with paired t-tests. $P45_{diff}$ was greater than zero for most movement phases, reflecting gating of the P45: pre-max speed ($t(33) = 2.78, p = 0.010, d_z = 0.48, 95\% \text{ CI } [0.18-1.13]$), early post-max speed ($t(33) = 4.18, p < 0.001, d_z = 0.72, 95\% \text{ CI } [0.47-1.36]$), and late post-max speed ($t(33) = 3.83, p < 0.001, d_z = 0.66, 95\% \text{ CI } [0.57-1.87]$). Importantly, $P45_{diff}$ was not significantly different from zero around maximum speed ($t(33) = 0.91, p = 0.367, d_z = 0.16, 95\% \text{ CI } [-0.32-0.83]$), indicating a transient recovery of early cortical processing around the onset of reach deceleration. These findings demonstrate gating of somatosensory signals during movement, except during the time when sensory guidance of the hand gains importance.

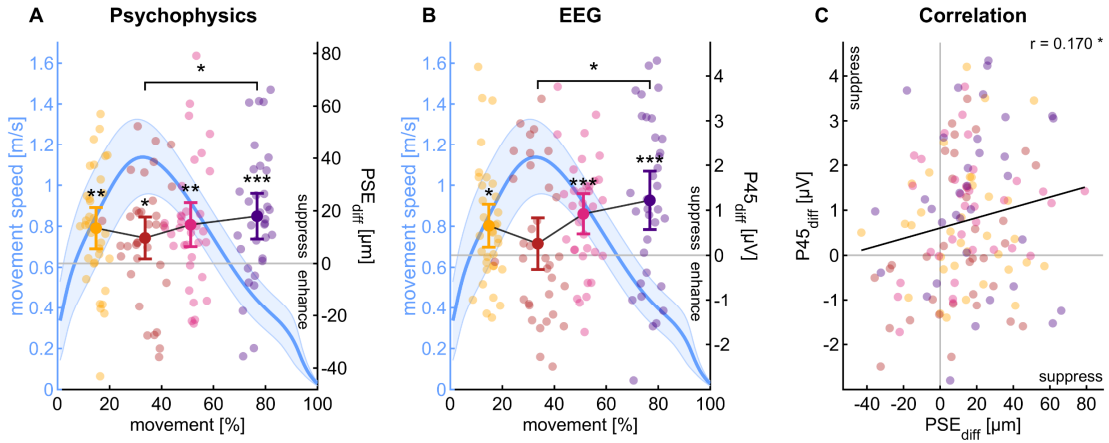


Fig. 4: Movement-related suppression in tactile perception and SEP amplitude.

Average time-normalized movement speed across participants ($n = 34$; blue line, left y-axis). Shaded area indicates standard error. The right y-axis shows mean PSE_{diff} (A) and P45_{diff} (B) for the four movement phases: pre-max speed (yellow), around max speed (red), early post-max speed (pink), and late post-max speed (purple). Error bars represent 95% confidence intervals. Dots illustrate individual participants. **A.** Tactile perception was suppressed in all four movement phases (paired t -tests against zero). Tactile suppression was weaker around max speed relative to the late post-max speed phase (univariate ANOVA, paired t -tests). **B.** P45 amplitude was comparable to rest around max speed and suppressed in all other movement phases (paired t -test against zero). P45_{diff} was smaller around max speed than in the late post-max speed phase, indicating less SEP gating mid-reach relative to later in the movement (univariate ANOVA, paired t -tests). **C.** Scatterplot of P45_{diff} versus PSE_{diff}. Each point represents one participant in one movement phase. The black line shows the pooled ordinary least squares regression of P45_{diff} on PSE_{diff} across all observations. Stronger tactile suppression during movement was significantly associated with lower P45 amplitude (Pearson correlation). $^* = p < 0.05$, $^{**} = p < 0.01$, $^{***} = p < 0.001$.

A repeated-measures ANOVA revealed a temporal modulation of P45_{diff} across movement phases ($F(3, 99) = 3.35$, $p = 0.044$, $\eta^2_p = 0.092$). Post-hoc t -tests showed significantly smaller P45_{diff} around max speed than in the late post-max phase ($t(33) = -2.53$, $p = 0.049$, $d_z = -0.43$, 95% CI [-1.73– -0.19]), supporting the recovery of processing around the time of maximum speed, consistent with the psychophysical results. No significant differences were observed in P45_{diff} between the other movement phases (all $t(33) \geq -2.41$, $p \geq 0.066$, $d_z \geq -0.41$; see Fig. 4B). Lastly, a significant Pearson correlation between PSE_{diff} and P45_{diff} ($t(134) = 2.00$, $p = 0.048$, $r = 0.170$, 95% CI [0.002–0.33]) revealed that stronger tactile suppression in the PSEs was associated with reduced P45 amplitudes (see Fig. 4C).

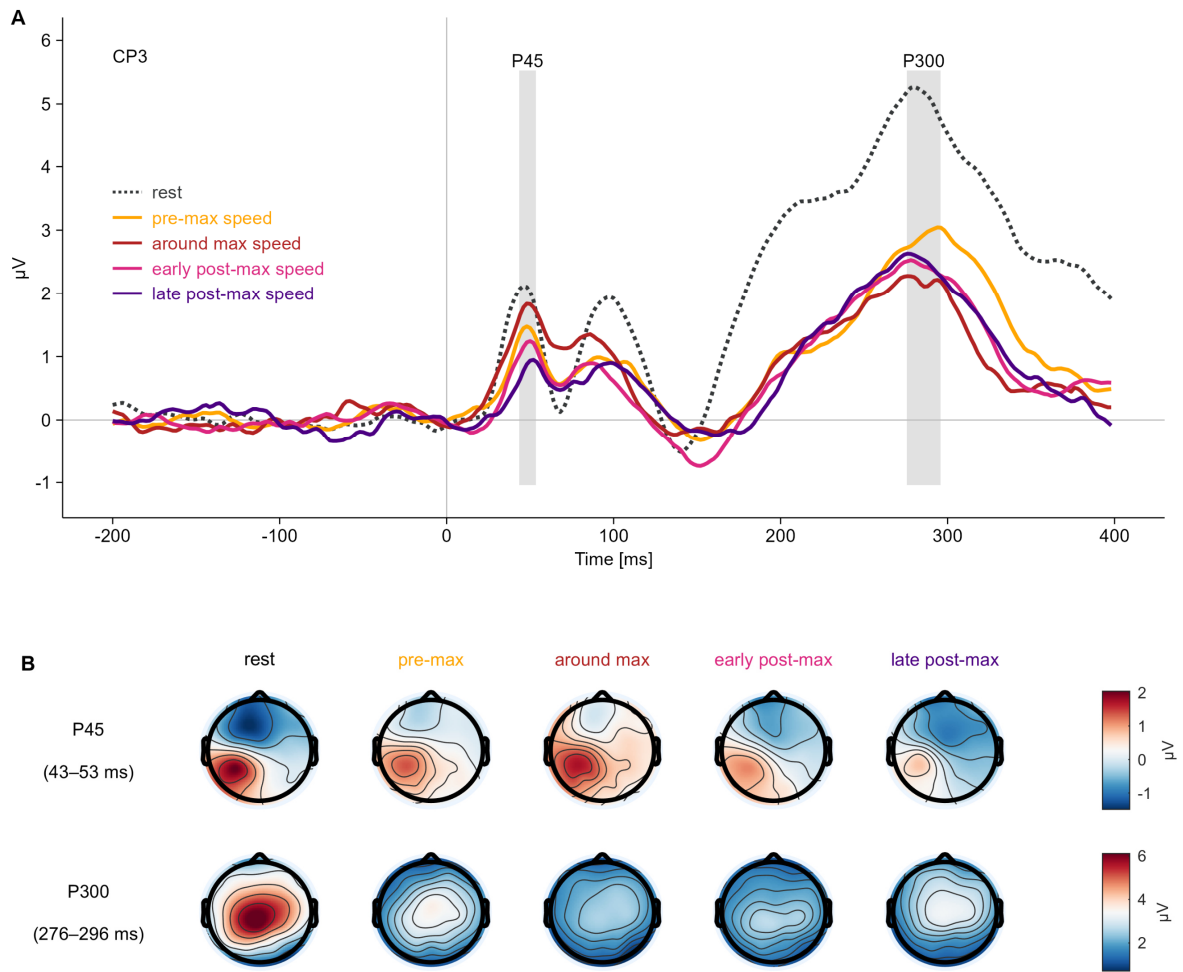


Fig. 5: Grand-averaged SEPs during rest and movement.

A. Grand-averaged SEPs at CP3 ($n = 34$), time-locked to standard vibration onset, with P45 and P300 highlighted. **B.** Scalp topographies for the P45 and P300 across the rest condition and movement phases.

Taken together, these findings suggest that early cortical processing contributes to the temporal modulation observed in tactile suppression during reaching. Perceptual reports, however, are shaped not only by early cortical processes, but also by higher-order cognitive mechanisms (e.g., stimulus evaluation and decision-making processes (Heekeren et al., 2008)).

To test whether later cortical mechanisms likewise exhibited dynamic changes across the movement, we also examined SEP gating in the P300 component (see Fig. 5). $P300_{diff}$ was significantly greater than zero in all phases, reflecting consistent gating of the P300 throughout

the movement: pre-max ($t(33) = 3.97, p < 0.001, d_z = 0.68, 95\% \text{ CI } [1.03\text{--}3.21]$), around max ($t(33) = 3.95, p < 0.001, d_z = 0.68, 95\% \text{ CI } [1.22\text{--}3.81]$), early post-max ($t(33) = 4.81, p < 0.001, d_z = 0.82, 95\% \text{ CI } [1.51\text{--}3.72]$), and late post-max ($t(33) = 2.85, p = 0.010, d_z = 0.49, 95\% \text{ CI } [0.68\text{--}4.04]$). Additionally, in contrast to the PSE_{diff} and P45_{diff} , the $\text{P300}_{\text{diff}}$ did not significantly differ between the four movement phases ($F(2.08, 68.59) = 0.43, p = 0.658, \eta^2_p = 0.013$), i.e., we found no temporal modulation at this later stage of somatosensory processing.

Discussion

We report temporal dynamics in tactile suppression during goal-directed reaching, with weaker suppression around maximum speed. This temporal modulation was paralleled in early somatosensory processing. As expected, P45 amplitudes were reduced during most movement phases relative to rest, reflecting early cortical gating (Rossini et al., 1999; Rushton et al., 1981). However, P45 responses near maximum speed were comparable to rest and larger than late in the movement. These reductions in P45 amplitude correlated with stronger tactile suppression, suggesting a link between changes in tactile sensitivity during movement and early somatosensory processes. In contrast, P300 amplitudes were uniformly reduced during movement. This suggests that the temporal modulation reflects sensorimotor rather than cognitive processes. Our findings are consistent with reports of phase-dependent sensory modulation during goal-directed movements (Česonis & Franklin, 2020; Dimitriou et al., 2013; Wachsmann et al., 2025a). Similarly, a previous study using the same task reported a complete release from suppression in this movement phase, with tactile sensitivity around maximum speed matching sensitivity at rest (Voudouris & Fiehler, 2021). In contrast, we observed tactile suppression across all movement phases, including maximum speed. This discrepancy may reflect differences in psychophysical task demands: earlier work used a binary detection response immediately after movement offset (Voudouris & Fiehler, 2021), whereas our delayed comparison task required stimulus retention until several seconds after movement completion.

Consistent with this, the P300, which is sensitive to memory load (Polich, 2007), was uniformly gated across all movement phases, suggesting that cognitive load may have sustained perceptual suppression, even at phases of preserved early processing. However, the P45 component, a temporally precise index of sensory encoding tied to low-level stimulus features such as intensity (Fuehrer et al., 2025; Schröder et al., 2021), was preserved around maximum speed. Thus, despite stronger overall perceptual suppression in our task, both studies converge on a transient release from suppression around maximum speed. These findings provide a crucial link between perceptual modulation during movement and changes in early sensory processing. Our results align with optimal feedback control accounts, which propose a state-dependent modulation of feedback gains during movement (Liu & Todorov, 2007; Todorov & Jordan, 2002). Consistent with this, visuomotor gains peak mid-reach and decrease upon approaching the target (Dimitriou et al., 2013). Tactile signals contribute to the transport phase of reaching (Gentilucci et al., 1997), possibly by providing proprioceptive guidance (Aimonetti et al., 2007; Moscatelli et al., 2019). Thus, reduced tactile suppression around maximum speed may reflect a transient upregulation of somatosensory feedback during the transition from movement initiation to feedback-driven deceleration (Elliott et al., 2001). Alternatively, the effect could reflect stronger late suppression as the motor system shifts from position control to movement termination or anticipates target contact (Fraser & Fiehler, 2018; Liu & Todorov, 2007). However, mid-reach P45 amplitudes were comparable to rest, but gated in both earlier and later phases, arguing against a purely late-suppression account and supporting selective preservation of early processing when feedback demands are highest.

The mid-reach reduction in tactile suppression contrasts with reports of higher movement speed increasing suppression (Angel & Malenka, 1982; Cybulska-Klosowicz et al., 2011) and reducing cortical responses (Chapman et al., 1988; Rushton et al., 1981), perhaps due to stronger reafferent masking (Laskin & Spencer, 1979). However, those studies involved

isolated joint movements with minimal precision demands. In contrast, suppression during complex movements requiring precision appears unaffected by increased reafferent input from stronger forces (Broda et al., 2020). In our somatosensory-guided task without visual feedback, tactile input likely became more relevant just before the deceleration phase. These findings indicate that suppression is not merely a function of movement parameters like speed, but depends on the task relevance of somatosensory input. This aligns with previous evidence of modulations in short-latency SEPs by movement demands in balancing and precision tasks (Knecht et al., 1993; McIlroy et al., 2003; Wasaka et al., 2017). Similar phase-dependent modulation has been reported in locomotion (Altenmüller et al., 1995; Chapin & Woodward, 1982; Duysens et al., 1990; Mouchnino et al., 2015). Our results further support the link between neural changes and perception by demonstrating phase-dependent SEP modulation during somatosensory-guided reaching.

Unlike traditional SEP paradigms using transcutaneous nerve stimulation (Cruccu et al., 2008), we applied vibrations in the preferred range of Pacinian mechanoreceptors and rapidly adapting type II (RAII) fibers (Bolanowski et al., 1988). This allowed the examination of early cortical responses to naturalistic, low-threshold mechanoreceptor signals, rather than synchronized mixed-fiber activation (Gardner et al., 1984). While the stimulation primarily engaged Pacinian mechanoreceptors, reaching likely generated input from a range of cutaneous and proprioceptive receptors. The P45 component arises mainly from S1 (Allison et al., 1992), which has been associated with early cutaneous-proprioceptive integration (Kim et al., 2015). The observed modulation may therefore reflect broader regulation of somatosensory input, beyond RAII-specific tuning.

Since movement-related gating of somatosensory responses has been documented at multiple stages of the ascending pathway, from first-order synapses in the spinal dorsal column to thalamic nuclei (Chapman et al., 1988; Ghez & Pisa, 1972; Seki & Fetz, 2012), the reductions

in P45 amplitude observed here may reflect decreased afferent inflow into S1. At the spinal level, gating is mediated by presynaptic inhibition via local interneurons (Bui et al., 2015). In primates, this presynaptic inhibition is partly driven by descending pathways from the brainstem and cortex and emerges before EMG onset (Seki et al., 2003). Consistent with this, in the rodent whisker system, movement-related gating at the first synaptic stage is abolished when S1, S2, and posterior parietal cortex are lesioned, indicating top-down control of sensory gating already at the first synaptic stage (Chakrabarti & Schwarz, 2018). Converging evidence from humans likewise implicates S1, S2, posterior parietal cortex, and supplementary motor area in downregulating somatosensory perception during movement (Arikan et al., 2021; Haggard & Whitford, 2004). Although descending pathways are likely involved in regulating presynaptic inhibition, stronger gating at cortical than spinal levels in primates suggests additional cortico-cortical modulation (Seki & Fetz, 2012). For example, the motor cortex can recruit inhibitory neurons in the rodent auditory cortex to attenuate self-generated sounds (Schneider et al., 2018), illustrating how motor-related signals can engage local inhibitory circuits in the sensory cortex. Together, these findings support cortical control of tactile feedback gains, with descending pathways regulating afferent inflow and intracortical circuits modulating early cortical responses. The transient mid-reach release from P45 gating may therefore reflect reduced presynaptic inhibition along the pathway, decreased intracortical inhibition, or both. Resolving this will require combined cortical and subcortical measures. These gating mechanisms operate within a bidirectional sensorimotor control loop in which motor commands shape sensory inflow and somatosensory feedback influences motor output (Azim & Seki, 2019). Cutaneous and proprioceptive signals tune reflexes and shape ongoing movements by regulating motoneuron excitability via spinal interneuron circuits (Bui et al., 2015; Panek et al., 2014). Disrupting presynaptic inhibition of proprioceptive afferents impairs goal-directed reaching in rodents (Fink et al., 2014), whereas blocking cutaneous input

increases hand path variability in grasping (Gentilucci et al., 1997), indicating that both excessive and absent somatosensory feedback compromise motor control. Together, these findings suggest that sensory gain is dynamically tuned to task demands. The modulation in early cortical gating observed here likely reflects such adjustments of reafferent gain, suppressing redundant somatosensory input while allowing behaviorally relevant feedback to influence motor circuits (Azim & Seki, 2019). Consequently, changes in perceived tactile intensity during movement may represent the behavioral expression of this distributed sensorimotor gating (Azim & Seki, 2019; McComas, 2016).

Limitations

One limitation concerns potential overlap of SEPs with task-related events such as movement offset and target contact. This overlap would primarily affect the later P300, whereas the earlier P45 likely occurred during ongoing movement. Because these events were not systematically aligned with stimulation timing, any influence should be random and contribute as noise rather than as systematic bias. To mitigate these effects, we subtracted the EEG signal recorded during reaching alone from that recorded during reach with stimulation. The subtracted signal was time-locked to the corresponding stimulation timing post movement onset and therefore included the same unsystematic movement-related activity present during the stimulation epochs. This approach assumes an additive relationship between movement- and stimulation-related signals, although prior work has questioned this assumption (Quinn et al., 2014). Nevertheless, the resulting SEP waveforms matched canonical patterns reported for vibrations, including a fronto-parietal dipole for the P45, and a centro-parietal positivity for the P300 (Alouit et al., 2025; Fuehrer et al., 2025), supporting the validity of the method.

Conclusion

In sum, tactile suppression is temporally tuned, with a distinct reduction around maximum speed. This modulation was accompanied by changes in early somatosensory processing,

suggesting preserved S1 engagement when somatosensory input from the moving limb is most relevant for the sensory guidance of the hand. This pattern suggests a flexible tuning of suppression and gating according to task demands. Higher-order processes appear to contribute to a general dampening of tactile perception but not to its fine-grained temporal tuning. This novel relation of psychophysical modulation to early neural markers underscores that tactile suppression is a flexible, context-sensitive mechanism coupled to sensorimotor demands.

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Competing interests

Authors declare that they have no competing interests.

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