Mechanisms of sensory attenuation and enhancement in auditory and tactile perception

Inaugural-Dissertation

Zur Erlangung des Doktorgrades

der Mathematisch-Naturwissenschaftlichen Fakultät

der Heinrich-Heine-Universität Düsseldorf

vorgelegt von

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Düsseldorf, Mai 2026

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Gedruckt mit der Genehmigung der
Mathematisch-Naturwissenschaftlichen Fakultät der
Heinrich-Heine-Universität Düsseldorf

Berichterstatter:

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Tag der mündlichen Prüfung: 16.07.2026

Contents

List of Figures

Summary

Humans are exposed to a multitude of stimuli in their daily lives. To be able to discriminate between different incoming stimuli, theories have proposed the phenomenon of sensory attenuation, suggesting that self-generated stimuli are perceived differently from similar externally generated ones. According to prominent approaches, this effect is based on efference copies of motor commands that are only available to the person performing the action. These efference copies are used in forward models, in which the predicted and the actual sensory outcome are compared and, in case of a match, attenuated. However, these approaches have recently been challenged by studies that also found attenuated perception without the involvement of self-generated actions. In addition, some studies failed to find attenuation following self-generated stimuli and instead reported enhanced perception. In this dissertation, the role of active movement was investigated in comparison to passive but temporally predictable movement. Furthermore, the seemingly opposing findings of attenuation and enhancement were examined by using different stimulus intensities. Study 1 revealed that the effects of sensory attenuation and enhancement in the auditory domain depend on stimulus intensity. Quiet tones tended to be enhanced, whereas louder tones were perceived as attenuated, resulting in a regression-to-the-mean pattern. It was further shown that this perceptual mean can be shifted by adapting participants to either loud or quiet contexts. When unexpected intensities were presented, participants showed stronger attenuation or enhancement in the direction of the adapted context. Moreover, this regression effect was also observed in conditions without participants' actions but with visual cues that rendered the tone temporally predictable. In Study 2, the reported origins of the regression effect in Study 1 were investigated to examine why prediction or self-generation of a stimulus leads to perceptual biases rather than increased precision. It was found that the involvement of predictive cues or actions draws attention away from the perceived stimulus. This form of distraction increases uncertainty, resulting in a stronger regression toward the mean. Study 2 showed that prediction per se is not the crucial factor underlying auditory regression effects but rather constitutes one source of diverted attention that gives rise to this pattern. In Study 3, the role of predictability compared to action was investigated in the tactile domain. Participants moved either actively or passively along a trajectory that ended at a position in which self-touch was induced. After finding no differences in the perceived intensity between active and passive conditions, the passive conditions were further examined regarding different aspects of predictability. After experimentally excluding visual and (spatio-)temporal predictability as well as the sense of agency, proprioceptive predictability emerged as the crucial factor. It was further shown that proprioceptive predictability can be used to recalibrate the perception of self-touch. Specifically, even when the position of touch delivery was shifted away from the touched finger, attenuated perception was still observed, suggesting that participants' representation of their arm in space had been recalibrated. In summary, auditory attenuation and enhancement can be understood as facets of a regression-to-the-mean pattern that arises due to a lack of attention caused by self-generation or predictive cues. Tactile attenuation of self-touch appears to result from proprioceptive predictability and can be recalibrated. Future research should investigate the regression effect in the tactile domain, as well as the role of attention in this modality, and examine parallels and differences between behavioral and neurophysiological findings across both modalities.

1 General Introduction

Humans rely on multiple sensory modalities to perceive and interact with their environment (e.g., Stein & Stanford, 2008; Zhaoping, 2023). Accordingly, sensory systems continuously encode vast amounts of information: for example, the human retina may transmit visual information at a rate of several million bits per second, roughly comparable to an Ethernet connection (Koch et al., 2006). Among the senses, vision plays a particularly dominant role for human perception, with a substantial proportion of the cortex dedicated to visual processing and a large network of specialized areas supporting perception and behavior (e.g., Grill-Spector & Weiner, 2014; Hubel & Wiesel, 1962). Importantly, perception does not rely on a single modality but emerges from the integration of multiple sensory inputs, allowing for coherent representations of the environment and flexible, adaptive behavior. The coordination of seeing, hearing, touching, tasting, and smelling enables humans to effectively interact with their environment and with each other. Over millions of years, sensory systems have been shaped to efficiently encode behaviorally relevant information from the environment (e.g., Manning et al., 2024; Oteiza & Baldwin, 2021). This dissertation will mainly focus on the senses of hearing and touch, which will now be elaborated further.

1.1 Hearing

Next to vision, audition is one of the primary sensory modality that enables the perception of events from distance. The auditory system therefore plays a central role in spoken communication and is particularly sensitive to frequencies in the range of human speech (1–4 kHz), where frequency discrimination is especially accurate (e.g., Oxenham, 2012). Sound localization is supported by binaural cues, as sounds arrive at the two ears with slight differences in timing and intensity as well as by spectral filtering through the outer ear, which contributes to spatial hearing (e.g., Blauert, 1996). Sound intensity is typically expressed in decibels (dB), a logarithmic scale that can be adjusted to reflect human hearing sensitivity, with normal conversation occurring around 60 dB and levels above approximately 120 dB approaching the pain threshold. In response to high-intensity sounds, middle ear muscles can contract and reduce the transmission of sound energy to the inner ear, avoiding damages (Schandry, 2016). At the cortical level, the primary auditory cortex is organized tonotopically with systematic representations of sound frequency (Rauschecker & Scott, 2009). Early stages of auditory processing occur rapidly, with neural responses emerging within approximately 70–100 ms after stimulus onset, as reflected in components such as the auditory N1, an event-related potential (ERP) component associated with the early cortical encoding of auditory stimulus properties (e.g., Näätänen & Picton, 1987).

1.2 Feeling and Proprioception

The skin is the largest sensory organ of the human body and forms a primary interface with the external environment through the sense of touch (Birbaumer & Schmidt, 2010). Somatosensation provides information about the body, including the skin, musculoskeletal system, and internal organs, and is commonly divided into exteroception (signals from the body surface), proprioception (information about body position and movement), and interoception (signals from internal organs; Craig, 2002). While vision and audition are mainly specialized for the detection of distal stimuli, the somatosensory system processes information through direct physical contact and internal bodily signals.

The sense of touch enables the perception of object properties such as shape, texture, and surface structure through direct contact. This modality includes sensations such as pressure, vibration, temperature, and pain, which are mediated by different types of specialized receptors in the skin, including Merkel cells, Meissner corpuscles, Pacinian corpuscles, Ruffini endings, and free nerve endings (Johnson, 2001). These receptors differ in their adaptation properties and functional roles. Slowly adapting mechanoreceptors, such as Merkel and Ruffini afferents, respond to sustained stimulation and are important for encoding pressure and form. In contrast, rapidly adapting receptors, such as Meissner and Pacinian corpuscles, respond primarily to changes in stimulation and are particularly sensitive to dynamic touch, such as skin motion and vibration (Vallbo & Johansson, 1984). Pacinian corpuscles are especially sensitive to high-frequency vibrations (approximately 50–700 Hz), whereas Meissner corpuscles respond preferentially to lower frequencies (e.g., Hollins et al., 2000).

Receptive fields refer to the regions of skin over which stimulation influences the activity of a specific sensory neuron. Their size varies across receptor types: Merkel and Meissner afferents have small receptive fields of less than 1 mm diameter, enabling high spatial resolution, whereas Pacinian and Ruffini afferents can span areas as large as a finger (Johnson, 2001; Schandry, 2016). Spatial resolution also varies across the body surface, with the highest resolution at the fingertips and lips, where two-point discrimination thresholds can be as low as 1–3 mm, compared to much larger thresholds of 3–4.5 cm on areas such as the calf (Stevens & Choo, 1996). When stimuli are presented simultaneously, the two-point threshold is typically higher (Birbaumer & Schmidt, 2010).

In touch, all cutaneous sensations are projected onto somatotopically organized maps in the somatosensory cortex. However, tactile perception is not limited to identifying where on the skin a stimulus occurs. For example, when searching for a light switch in a dark room, one may be aware of which part of the hand is stimulated, but the primary goal is to localize the object in external space (Longo et al., 2015). To achieve this, the nervous system must integrate tactile information with proprioceptive signals about body posture and limb position (Yamamoto & Kitazawa, 2001). This integration allows tactile events, initially encoded in a skin-based (somatotopic) reference frame, to be remapped into external spatial coordinates (de Haan et al., 2012; Haggard et al., 2006; Medina & Coslett, 2010). This process, known as tactile spatial remapping, is essential for external spatial localization (Longo et al., 2015).

The role of proprioception is essential but not uniformly defined (Hillier et al., 2015). It is generally described as a combination of perceptual abilities, including the perception of joint position (Niessen et al., 2009; Ogard, 2011; Proske, 2006), force and muscular effort (Proske, 2006; Proske & Gandevia, 2012), movement and kinesthesia (Ogard, 2011; Proske & Gandevia, 2012), as well as velocity, acceleration, and heaviness (Proske, 2006). These signals are mediated by specialized mechanoreceptors, including muscle spindles, Golgi tendon organs, and joint receptors, which continuously monitor the state of the musculoskeletal system. Muscle spindles signal changes in muscle length, whereas Golgi tendon organs encode muscle force (Proske & Gandevia, 2012). Proprioceptive information is conveyed via ascending pathways in the spinal cord, with projections to the cerebellum supporting sensorimotor coordination and to the thalamus and somatosensory cortices supporting conscious perception (Johansson & Flanagan, 2009).

The interaction between tactile and proprioceptive signals becomes particularly evident when these signals are experimentally manipulated. For example, crossing the hands over the body midline creates a mismatch between anatomical and external spatial reference frames. In such

conditions, a tactile stimulus delivered to the right hand is perceived in the left hemispace, leading to a conflict between reference frames and a decrease in performance in temporal order judgment tasks, which is known as the crossed-hands deficit (Heed & Azañon, 2014; Shore et al., 2002; Yamamoto & Kitazawa, 2001). This paradigm has been used to investigate the integration of somatotopic and external spatial representations (Azañón & Soto-Faraco, 2008; Heed & Röder, 2010; Overvliet et al., 2011).

The integration of tactile and proprioceptive information is also closely linked to body ownership. In the rubber hand illusion, synchronous multisensory stimulation can induce the feeling that a rubber hand belongs to one's own body (Botvinick & Cohen, 1998; Ehrsson et al., 2004; Lloyd, 2007). This illusion demonstrates that visual information often dominates proprioceptive signals, leading to a recalibration of perceived hand position. Variants of the rubber hand illusion have shown that similar effects can occur even in the absence of vision (Ehrsson et al., 2005; Petkova et al., 2012), although vision typically strengthens the effect (Botvinick & Cohen, 1998). Crossing the hands during such paradigms can further modulate the illusion by altering the integration of tactile and proprioceptive cues. While some studies report increased illusory self-touch under these conditions (Pozeg et al., 2014), others have found reduced proprioceptive drift, suggesting that conflicting signals can impair multisensory integration (Rohde et al., 2011).

In addition to cutaneous input, deep somatosensory signals from muscles, tendons, and joints contribute to the perception of body position and movement. Movement can be understood as the displacement of body tissues over time (Schandry, 2016), and its perception relies on the integration of motor commands with incoming sensory feedback. A special case of somatosensory processing is self-touch, in which the body simultaneously acts as both the source and the recipient of stimulation. In such situations, motor signals, proprioceptive feedback, and tactile input are tightly integrated (Ernst & Banks, 2002; Tsakiris, 2017). For example, when one hand touches the other, the brain combines information about the executed movement with tactile signals from both the acting and receiving body parts, resulting in a coherent perception of the event and the body in space (Ehrsson, 2020), which is essential for goal-directed actions or interactions with the environment (Wolpert et al., 1995).

1.3 Multisensory integration

Multisensory integration refers to the process by which information from different sensory modalities is combined into one coherent percept (Stein & Stanford, 2008). Because signals from different senses often occur simultaneously, the brain must determine whether they originate from a common source and should be integrated or not. This integration typically goes beyond a simple summation of sensory inputs (Stein & Stanford, 2008) and is instead well described by statistically optimal weighting, in which each modality contributes according to its relative reliability (Ernst & Banks, 2002).

In spatial perception, for example, information about body position can be derived not only from proprioception but also from vision, requiring the integration of these signals into a common reference frame (Ehrsson, 2020; Ernst & Banks, 2002). Importantly, multisensory integration is flexible and influenced by additional factors such as attention, task demands, and prior expectations (Macaluso et al., 2016). In many situations, visual information tends to dominate perception, particularly when it provides more precise or reliable spatial cues. This phenomenon, often referred to as visual dominance, becomes especially apparent in situations of sensory conflict (De Gelder & Bertelson, 2003). In such situations, the information of the most accurate

sense is weighted more, which creates a bias in the interpretation in favor of this information (Ernst & Banks, 2002).

A typical example of such conflicts is provided by bodily illusions, such as full-body illusions, an extension of the rubber hand illusion, in which participants view a virtual avatar being touched while simultaneously receiving tactile stimulation themselves. When visual and tactile signals are temporally and spatially congruent, participants may experience a shift in perceived body ownership toward the seen body (Bayer et al., 2023; Ehrsson, 2007; Lenggenhager et al., 2007). These findings illustrate how multisensory integration can bias perception toward the most reliable sensory input, often favoring vision in spatial tasks.

1.4 Sensory processing and perceptual biases

Despite the vast amount of sensory information available to the human brain, only a small part reaches conscious awareness. Estimates suggest that sensory systems can encode information at rates on the order of 10^8–10^9 bits per second, whereas conscious processing is limited to roughly 10 bits per second (Zheng & Meister, 2025). This discrepancy highlights that most incoming signals are processed unconsciously and must be selectively filtered. Efficient perception therefore requires mechanisms that prioritize relevant over irrelevant information while reducing the impact of redundant input.

A key distinction in this context is based on the difference between self- and externally generated sensory signals (Blakemore et al., 1998; Wolpert et al., 1995). Many of the sensory consequences of our own actions are highly predictable and carry little new information (e.g., Friston, 2010). For example, when a hand brushes against the body, the resulting tactile input does not require continuous conscious processing (Bays et al., 2006; Blakemore et al., 1998). In contrast, externally generated stimuli, such as a stranger tapping on our shoulder, are more likely to signal behaviorally relevant events and therefore demand attention (Friston, 2010).

The described phenomenon is commonly studied under the term *sensory attenuation*, which refers to the reduced perceived intensity of self-generated stimuli compared to externally generated ones. A prominent example used in established literature is the reduced ticklishness of self-produced touch compared to identical stimulation delivered by another person (Blakemore et al., 1998).

A classic example of sensory attenuation from the animal kingdom is provided by the electric fish, which generates electric fields for navigation and prey detection. To function effectively, these animals must filter or suppress self-generated signals to remain sensitive to external inputs (Bell, 2001; Bullock, 1982). This mechanism illustrates a general principle that is also observed in humans: predictable sensory consequences of one's own actions are attenuated to enhance the detection of behaviorally relevant external events (e.g., Blakemore et al., 2000; Crapse & Sommer, 2008). From an evolutionary perspective, sensory attenuation is useful since it saves resources by "down-weighting" sensory events from our own behavior to be more accurate in detecting potential threats from the outside, such as predators (Crapse & Sommer, 2008). While sensory attenuation has primarily been studied in the tactile domain (e.g., the reduced ticklishness of self-generated touch), the effect has also been demonstrated across sensory modalities, including audition (Sato, 2008; Weiss et al., 2011a) and vision (e.g., Cardoso-Leite et al., 2010; Storch & Zimmermann, 2022) with ambiguous findings (Schwarz et al., 2018). Sensory attenuation is commonly characterized as a reduction in perceived intensity or salience of self-generated stimuli, although recent work suggests that the exact expression of this effect is context-

dependent and more nuanced than originally assumed. Rather than a general suppression of self-generated input, perceptual processing can also be enhanced under certain conditions, depending on factors such as task relevance and intention (Press et al., 2020; Yon et al., 2021).

Contemporary accounts propose that perception is not a passive process but is fundamentally shaped by prediction. According to predictive processing frameworks, the brain continuously generates expectations about the sensory consequences of actions and compares them to incoming input (Friston, 2010). Predictable self-generated signals are down-weighted, allowing the system to remain sensitive to unexpected, potentially informative events (Limanowski & Friston, 2020; Parr & Friston, 2018), as it will be discussed further within this dissertation. As a self-organizing system, the human body has been proposed to be most intimately acquainted with self-related signal (Ciaunica et al., 2021). This implies that it is not a matter of selecting which sensory signal to emphasize, but rather which one to attenuate (Limanowski & Friston, 2020; Parr & Friston, 2018). Regarding this, perception is no passive receiving but rather an active and predicting process (Müsseler & Rieger, 2017). In the example of grasping a ripe cherry from a tree, we are more sensitive to the characteristics of the cherry than to the feelings of how our arm will get there while reaching, even though we know we need to perform the movement correctly to reach the goal (Limanowski & Friston, 2020).

1.5 Markers of sensory attenuation

At the neurophysiological level, sensory attenuation is frequently indexed by reduced event-related potentials (ERPs) measured with electroencephalography (EEG). ERPs reflect time-locked neural responses to sensory or cognitive events (Picton et al., 2000). They are used as a measure of the brain's processing of incoming sensory signals and thus commonly serve as measure for attenuation. In the auditory domain, the N1 component, which describes a negative deflection occurring approximately 80–120 ms after stimulus onset, is consistently reduced for self-generated compared to externally generated sounds (e.g., Ford et al., 2007; Mifsud & Whitford, 2017). This reduction has commonly been interpreted as reflecting predictive mechanisms that reduce neural responses to expected sensory consequences of one's own actions (e.g., Ford et al., 2007; Martikainen et al., 2005; Timm et al., 2013). However, some studies have suggested that temporal predictability contributes mainly to N1 attenuation effects and does not differ from self-initiated actions (e.g., Sowman et al., 2012).

Next to the N1 component, the P2 component peaks positively after 150–250 ms of stimulus presentation (Crowley & Colrain, 2004) and has also been associated with sensory attenuation effects (Klaffehn et al., 2019). However, the P2 and N1 effects are not always appearing equally strong within the same setups, which is why it has been suggested that they should be treated as distinct components (Bolt & Loehr, 2021; Crowley & Colrain, 2004; Egan et al., 2023; Klaffehn et al., 2019; Timm et al., 2016). In contrast to the comparatively robust and consistently replicated N1 suppression effect, findings regarding the P2 component appear to be more heterogeneous. While the N1 is thought to reflect early stages of sensory processing, including the encoding of basic acoustic features, P2 modulations have additionally been linked to attentional processes (Timm et al., 2013), agency and perceived control (Bolt & Loehr, 2021; Egan et al., 2023; Klaffehn et al., 2019), as well as temporal discrepancies between actions and sensory consequences (Weller et al., 2017). Accordingly, neurophysiological studies of auditory sensory attenuation have primarily focused on modulation of the N1 component (Korka et al., 2022). However, the P2 component has been shown to react more sensitively to self-specific actions that went beyond the attenuation of temporally predictable sounds (Bolt & Loehr, 2021).

Although neurophysiological and behavioral findings are often discussed under the common framework of sensory attenuation, both measures cannot necessarily be translated one-to-one. While neurophysiological attenuation reflects reduced neural responses (Bäß et al., 2008; Heinks-Maldonado et al., 2005; Heinks-Maldonado et al., 2006; Schafer & Marcus, 1973), behavioral attenuation captures changes in subjective perception (e.g., Weiss et al., 2011a). Recent work suggests that these two levels may rely on at least partially dissociable mechanisms, with their relationship additionally appearing to depend on the sensory domain (Giannini et al., 2025; Palmer et al., 2016). In contrast to neurophysiological markers, on the behavioral level, sensory attenuation is commonly assessed using psychophysical paradigms in comparison tasks (e.g., Sato, 2008). In auditory tasks, participants typically compare the perceived intensity of self-generated and externally generated tones. Measures such as the point of subjective equality (PSE) are used to quantify perceptual biases, with shifts in the PSE indicating changes in perceived intensity. PSEs can be extracted from psychometric functions or adaptive staircase procedures depending on participants' responses. A lower perceived intensity of self-generated stimuli relative to an unaffected baseline measurement or relative to the physically presented stimulus intensity is interpreted as attenuation, a higher one as enhancement. In addition, just noticeable differences (JNDs) can be derived to assess perceptual sensitivity, with larger JNDs indicating reduced discrimination ability. The higher the JND, the larger the difference required for two stimuli to be perceived as distinct (Weiss et al., 2011a).

Behavioral results in the auditory domain appear to be less consistent compared to reported neurophysiological N1 and P2 suppressions. While several studies report reduced perceived loudness for self-generated sounds (Sato, 2008; Weiss et al., 2011a), other work shows that this effect strongly depends on task design (Myers et al., 2020; Reznik et al., 2015). Thus, although neural attenuation in audition appears robust, its behavioral counterpart is more sensitive to contextual factors. Importantly, not all perceptions following self-generated actions point toward attenuation. For example, Reznik et al. (2015) demonstrated that near-threshold auditory stimuli can be detected more accurately when self-generated, suggesting perceptual enhancement under conditions of low stimulus intensity. At higher, clearly supra-threshold intensities of 74 dB, however, the typical attenuation pattern re-emerges.

A similar dissociation between neurophysiological and behavioral attenuation emerges in the tactile domain: neurophysiological attenuation has been observed for self-generated tactile stimulation (Blakemore et al., 1998; Palmer et al., 2016), again reflected in reduced evoked responses. However, Giannini et al. (2025) reported a clear attenuation in electrophysiological responses (reduced P2 amplitude) without any reduction in the behaviorally perceived intensity for tactile stimuli. Typical behavioral measures rely on force matching (Bays et al., 2006; Bays et al., 2005; Shergill et al., 2003), stroke (Blakemore et al., 1999; Schafer & Marcus, 1973), or haptic judgments (Fuehrer et al., 2022; Kiepe & Hesselmann, 2025), In force-matching paradigms, participants are asked to reproduce a previously experienced force. Those studies have shown that self-generated forces are systematically underestimated, leading participants to apply more force during reproduction, which is consistent with findings of a reduced perceived intensity of self-generated input (Bays et al., 2006). In social interaction paradigms with "tit-for-tat" exchanges in pairs of participants, this effect can lead to an escalation of applied forces across repeated exchanges: participants were instructed to apply the same force on the other participant as they have received themselves. It was shown that forces escalated quickly and in average about 3.2 N over eight turns, further illustrating the perceptual consequences of attenuation and underestimation of self-generated stimuli (Shergill et al., 2003). Giannini et al. (2025) criticize that the use of the explained behavioral measures are hardly adaptable to the temporal precision requirements of electrophysiological measures, which might be an explanation for ambiguous

findings. However, the differing findings across neurophysiological and behavioral studies suggest that sensory attenuation can occur independently of subjective perceptual changes. Similar to the auditory domain, this dissociation suggests that early sensory processing and subjective report are shaped by overlapping but not unified mechanisms (Press et al., 2020).

1.6 Approaches to explain sensory attenuation

The most prominent account proposed to explain sensory attenuation is the *forward model*. Originally, forward models were developed within theories of motor control and sensorimotor integration to explain how the nervous system predicts and monitors the sensory consequences of voluntary movements (Kawato, 1999; Miall & Wolpert, 1996; Wolpert et al., 1995). Within this framework, forward models are thought to contribute to action control by allowing the brain to estimate the expected sensory feedback of a movement before the actual sensory feedback becomes available. When performing an action, the brain generates motor commands to control the movement of muscles and limbs, specifying the desired action or trajectory (Kawato, 1999). According to the forward model framework, an efference copy of the motor command is generated and used by an internal forward model to predict the sensory consequences of the movement (Wolpert, 1997; Wolpert et al., 1995). The predicted sensory feedback can then be compared with the actual sensory feedback, allowing the system to detect discrepancies between expected and actual outcomes and thereby adjust ongoing or future movements (e.g., Blakemore et al., 1998; Heinks-Maldonado et al., 2005; Heinks-Maldonado et al., 2006; Wolpert et al., 1995). In cases of a mismatch, a prediction error is generated. Prediction errors can be either positive or negative: a positive prediction error indicates that the expected outcome was overestimated (e.g., a stronger touch or louder tone was predicted), whereas a negative prediction error reflects an underestimation of the actual outcome (e.g., a weaker touch or quieter tone was expected; Welniarz et al., 2021). It is assumed that the forward model continuously improves its accuracy by minimizing discrepancies between predicted and actual outcomes through ongoing adjustments (Miall & Wolpert, 1996). The forward model framework was later extended from motor control to perceptual phenomena such as self-produced touch. A prominent example is the inability to effectively tickle oneself (Blakemore et al., 1999; Blakemore et al., 1998). According to this account, self-generated tactile sensations are predicted on the basis of the motor command and are therefore perceived as less intense. In contrast, externally generated touch is less predictable and consequently perceived as more salient. Blakemore et al. (1998) demonstrated that self-produced tactile stimulation is perceived as less ticklish than externally produced stimulation and interpreted this finding as evidence for predictive attenuation mediated by forward models.

Based on these findings, the forward model framework was subsequently extended to broader sensory attenuation effects, proposing that predicted sensory consequences of one's own actions are perceived as less intense than externally generated sensory events. If the predicted and actual sensory outcomes match, the resulting perception is attenuated (e.g., Blakemore et al., 1998; Heinks-Maldonado et al., 2005; Heinks-Maldonado et al., 2006; Wolpert et al., 1995). Kilteni et al. (2019) demonstrated the adjustability of forward models by reporting that participants can learn to incorporate a consistent temporal delay of 100 ms between an action and its sensory consequence. After adaptation, sensory attenuation was observed specifically for the learned delay, but no longer for immediate action–outcome pairings. Without prior learning, the introduction of a delay between an action and its sensory consequence leads to a gradual reduction of attenuation as the delay increases (Blakemore et al., 1999). Together, these findings highlight the critical role of temporal prediction in sensory attenuation, indicating that the effect

depends not solely on action–outcome contingency but also on the precise timing of expected sensory consequences.

In relation to forward models, multiple brain regions contribute to the generation of motor actions and the processing of their sensory consequences. In the context of self-generated auditory stimuli, reduced neural responses have consistently been observed in auditory cortex, alongside activity in motor-related regions such as the supplementary motor area and in higher-order regions including the anterior cingulate cortex, which are implicated in prediction and performance monitoring processes (Ford et al., 2001; Martikainen et al., 2005). In addition, the cerebellum plays a central role in motor learning, coordination, control, and the fine-tuning of action–outcome relationships (Paulin, 1993; Wolpert et al., 1998). Within forward model accounts, the cerebellum is commonly assumed to contribute to the generation and updating of sensory predictions based on efference copies of motor commands, particularly with respect to the precise temporal structure of the expected sensory consequences (Kawato, 1999). The cerebellum appears to be part of a distributed network that supports the computation as well as refinement of occurring prediction errors (Synofzik et al., 2008).

Consistent with this view, manipulations of temporal delays between actions and their sensory consequences have been shown to increase activity in the anterior and posterior cerebellum with longer intervals leading to more neural activity (Arikan et al., 2019). Further support for cerebellar involvement comes from patient studies: Knolle et al. (2013) demonstrated that individuals with cerebellar impairments show reduced or absent attenuation effects in electrophysiological responses, such as a lack of the typical N1 suppression for self-generated sounds. This finding supports the approach that on a neurophysiological level the cerebellum is critically involved in comparing predicted and actual sensory feedback and in implementing the predictive mechanisms underlying sensory attenuation. Moreover, the generation of motor actions and associated predictions involves a network of motor-related brain regions, including the motor cortex and its connected areas (Svoboda & Li, 2018). The motor cortex, encompassing the primary motor cortex and the supplementary motor area, plays a central role in the initiation and control of voluntary movements. In addition to generating motor commands, these regions are closely linked to the prediction of the sensory consequences of actions, likely through their interaction with forward model mechanisms (Ikeda et al., 1992).

The forward model framework of sensory attenuation implies that attenuation should primarily occur for self-generated actions, as these involve motor commands and corresponding efference copies that enable precise prediction of sensory consequences. However, empirical findings challenge this strict interpretation. For instance, attenuation effects have also been observed for externally generated stimuli, particularly when these can be predicted based on the actions of others (Ghio et al., 2018). Sensory signals reach the brain with a certain delay due to neural transmission and processing constraints (Kawato, 1999). Actions are typically associated with predictable sensory consequences (Wolpert et al., 1995). Without such predictive mechanisms, coordinated behavior would become less stable and less smooth, as movements would rely solely on delayed feedback (Miall & Wolpert, 1996). Self-generated motor activity and perception are therefore closely intertwined rather than independent processes (Blakemore et al., 2000). Each action is accompanied by expectations about its sensory outcome. Consequently, perception itself is not purely reactive but inherently includes an anticipatory component (Clark, 2013; Friston, 2010).

Although the forward model is well-established and has received substantial empirical support (e.g., Bays et al., 2006; Blakemore et al., 1998; Kilteni & Ehrsson, 2020), it has been criticized on several grounds, including its complexity, limited specificity regarding neural implementation,

and its restricted explanatory scope with respect to cognitive influences on perception (Dogge, Custers, et al., 2019). In particular, the model struggles to account for findings showing attenuation in the absence of voluntary motor commands, such as during passive movements, as well as enhanced perception following self-generated actions (e.g., Desmurget & Grafton, 2000; Dogge, Custers, et al., 2019; Weller et al., 2017; Yon et al., 2018). In this context, Dogge, Custers, et al. (2019) argue that motor-based predictions are not a necessary condition for sensory attenuation, since non-motor predictions can lead to similar effects. Instead, they propose that attenuation reflects a more general predictive mechanism that is not restricted to self-generated movements but can also arise from non-motor sources of prediction. From this perspective, motor predictions represent only one instance of a broader predictive system that modulates perception. Further challenges to a purely motor-based account come from studies demonstrating that predicted stimuli can, under certain conditions, lead to enhanced rather than attenuated perception. Press et al. (2020) and Yon et al. (2018; 2021) report that expected tactile stimuli are perceived as more intense or are biased toward predicted outcomes, suggesting an increased perceptual weighting of expected sensory input rather than a simple reduction in sensory processing. Importantly, these findings challenge the assumption that prediction through self-generation necessarily leads to attenuation. Supporting this view, Reznik et al. (2015) demonstrated that both enhancement and attenuation can occur within the same experimental paradigm, depending on stimulus intensity. Specifically, self-generated near-threshold stimuli were perceived as enhanced, whereas supra-threshold stimuli showed the typical attenuation pattern. Together, these findings suggest that sensory attenuation cannot be fully explained by forward models alone but instead reflects a more flexible, context-dependent mechanism embedded within a broader predictive framework (Dogge, Custers, et al., 2019).

According to *predictive coding* accounts, perception is understood as an inferential process aiming to minimize prediction errors through the integration of prior expectations and incoming sensory input. When sensory input closely matches prior predictions, only a small prediction error is generated, reflecting the reduced informational value of expected input. Because self-generated stimuli typically allow precise predictions about their sensory consequences, the resulting sensory input often closely matches these predictions, thereby generating only small prediction errors. Within this framework, the brain continuously uses prior knowledge to generate predictions about upcoming events (e.g., Clark, 2013; Friston, 2003, 2005; Huang & Rao, 2011; Rao & Ballard, 1999). The predictive coding framework is a generative model that consists of a set of neural representations that encode predictions about the background of sensory input at different levels. Predictive coding models conceptualize the brain as a hierarchical generative system, in which different levels of processing encode increasingly abstract representations of the causes of sensory input (Clark, 2013). At the lowest level, sensory representations encode incoming raw data, such as visual, tactile, or auditory information. Higher levels provide more abstract representations that encode predictions about the causes of the arrived inputs (Rao & Ballard, 1999). If prediction errors are high, the representation needs to update its predictions (Friston, 2008). This updating is divided into two types of signals that define predictive coding: first, prediction signals flow from higher to lower level representations and second, the prediction error signals flow from lower to higher level representations back (Grill-Spector & Malach, 2004). The top-down signals convey predictions about the causes of sensory inputs, while the prediction error signals convey bottom-up information about the mismatch between the predicted and the actual sensory inputs.

Importantly, within predictive coding frameworks, reduced neural responses to predicted stimuli are interpreted as reflecting reduced prediction error signals when sensory input matches prior predictions, rather than the operation of a dedicated cancellation mechanism based on

efference-copy computations (Friston, 2005, 2010; Kilner et al., 2007). In contrast to forward model accounts, predictive coding does not necessarily require efference copies or motor commands; instead, sensory attenuation can arise from highly predictable sensory input, regardless of whether predictions are generated through action or other sources (Friston, 2010; Kilner et al., 2007).

Notably, Press et al. (2020) argue that a reduced neural response does not necessarily result in a perceptually reduced response of participants. A predicted sensory outcome might lead to a smaller neural signal, but can also be perceived as enhanced after having taken into account Bayesian priors. Bayesian principles are fundamental to predictive coding frameworks, but they have also been used more broadly to explain perceptual enhancement effects following self-generated sensations (Thomas et al., 2022). Following this interpretation, perception is rather drawn towards what is expected, leading to more precise decisions. Expected events can be perceived as more intense, when prior expectations are combined with sensory evidence to generate interpretations, which is consistent with upweighting principles. Following this logic, we increase the accuracy of our perceptual representations by biasing them in line with prior expectations (e.g., expecting to encounter a polar bear in the arctic, Dayan & Jyu, 2003; de Lange et al., 2018). Yon et al. (2021) found that observes were biased to report the presence of expected action outcomes over unexpected ones. It is criticized that classical down-weighting or cancellation theories like the forward model are not able to explain enhancement effects, which is required. According to Thomas et al. (2022), predictive mechanisms must be able to generate up- and down-weighting processes, which occur under different circumstances that have to be taken into account. Extending predictive coding frameworks, within active inference accounts, movements are not primarily understood as actions that are first executed and then followed by predictions of their sensory consequences. Instead, the brain is proposed to generate predictions about a desired proprioceptive body state, while reflex-like motor mechanisms act to bring the actual body state in line with these predictions (Brown et al., 2013; Friston, 2010). According to this framework, sensory attenuation reflects a necessary reduction in the precision weighting of sensory evidence during movement, allowing proprioceptive predictions that drive movement to dominate ongoing sensory input. Consequently, sensory attenuation is interpreted not as a direct cancellation of self-generated sensory signals, but rather as a temporary down-weighting of sensory evidence that enables action execution. Brown et al. (2013) further proposed that failures of this attenuation process may contribute to disturbed agency attribution, because overly precise sensory signals could interfere with distinguishing between self-generated and externally generated sensory events.

An approach that aims to reconcile the roles of self-generated actions and more general predictive processes in explaining sensory attenuation is the *hybrid model* proposed by Dogge, Custers, et al. (2019). This model assumes that sensory attenuation arises from the interaction of multiple mechanisms rather than a single underlying process relying on self-generation. One such mechanism involves motor-based predictions, as described in the classical forward model framework (Wolpert et al., 1995). However, the hybrid model explicitly states that this mechanism is neither necessary nor sufficient on its own but rather represents one component within a broader predictive system. Crucially, the model proposes that attenuation can also emerge from non-motor sources of prediction, indicating that sensory attenuation may reflect a general mechanism of predictive processing that is not restricted to motor-based predictions. The effect may also arise whenever a sensory outcome is sufficiently predictable, regardless of whether this prediction is generated through motor commands, learned associations, or higher-level expectations such as goals or beliefs (Dogge, Custers, et al., 2019). The model further proposes that intentions about the sensory consequences of an action do not act as direct causal factors

but instead contribute indirectly by shaping predictions about expected sensory consequences, which in turn modulate perceptual processing.

Within the *ideomotor theory*, actions are assumed to be represented in terms of their anticipated sensory consequences. Performing an action to produce a specific outcome, like pressing a key to trigger a doorbell sound, automatically activates an internal representation of that effect (Greenwald, 1970; Hommel et al., 2001). According to this framework, actions and their perceptual effects are tightly linked through learned action-effect associations, such that activating the representation of an effect can also facilitate the corresponding action. When an action is performed, the anticipated sensory consequence is pre-activated, leading to a partial overlap between the predicted and the actual sensory representation. As a result, the actual sensory input contains less novel information and elicits a reduced increase in neural activity compared to unexpected stimuli. In this sense, sensory attenuation can be understood as a consequence of this representational overlap rather than as the result of an explicit cancellation or suppression mechanism. Importantly, ideomotor theory does not require a detailed motor-based forward model with efference copies. Instead, it assumes that well-learned action-effect associations are sufficient to generate predictions about sensory outcomes. These associations can be acquired through experience and can, in principle, operate independently of specific motor commands, as long as a reliable link between an action and its sensory consequence has been established (Pfister et al., 2014).

1.7 Factors influencing sensory attenuation

Alternative explanations for the occurrence of sensory attenuation propose that the effect may, at least in part, reflect shifts in *attention* rather than purely predictive mechanisms. According to this view, performing an action directs attentional resources toward the action itself and away from its sensory consequences (Saupe et al., 2013). As a result, these consequences may be processed less precisely, leading to an apparent attenuation effect. In addition to predictive processes, attention has been shown to systematically influence early sensory processing, including the N1 component of the auditory ERPs (Lange, 2013). On the other hand, Timm et al. (2013) published an ERP study suggesting that attenuation effects are independent from attention. According to a model addressing an interacting role of prediction and attention (Lange, 2013), attention enhances the processing of task-relevant stimuli, resulting in increased N1 amplitudes, whereas prediction reduces processing demands for expected stimuli, leading to decreased N1 amplitudes. In a behavioral detection task, Cao and Gross (2015) first showed that attended stimuli elicited increased neural responses and were detected more easily. However, when attention and sensory attenuation occurred simultaneously, the facilitatory effect of attention was reduced but remained significant. Based on these findings, the authors argued that attentional processes may play a substantial role in shaping attenuation effects.

In general, attention is commonly divided into endogenous and exogenous forms (Corbetta & Shulman, 2002; Desimone & Duncan, 1995; Posner, 1980). Endogenous attention refers to top-down processes in which attentional resources are voluntarily allocated according to internal goals, expectations, or task instructions. In contrast, exogenous attention is driven by bottom-up processes, whereby attention is automatically captured by salient or unexpected stimuli in the environment (Desimone & Duncan, 1995; Egeth & Yantis, 1997).

Regarding perception, endogenous attention has been shown to enhance sensory processing and perceptual sensitivity and may therefore modulate sensory attenuation effects (Coull et al., 2000; Coull & Nobre, 2008). For instance, when individuals are instructed to attend to self-generated

stimuli, this can increase perceptual awareness and processing of these stimuli, potentially leading to reduced attenuation effects due to enhanced processing of the sensory consequence. In contrast, exogenous attention may influence processing depending on stimulus order and salience: if a surprising or unexpected external stimulus captures attention, it may interfere with the processing of self-generated stimuli, thereby altering attenuation effects (Hughes et al., 2013).

Consequently, attention can modulate sensory attenuation in multiple ways. In some cases, attentional allocation may increase the perceptual contrast between self-generated and externally generated stimuli, thereby influencing the magnitude of attenuation (Eimer & Driver, 2001; Hughes et al., 2013). In other cases, attentional capture by external events may disrupt the processing of self-generated stimuli, leading to altered attenuation effects. A study by Fritz et al. (2022) demonstrated that the presentation of tactile feedback in the acting hand appears to be a necessity for attenuation effects at a passive finger, to which stimuli are presented. They concluded that processing a tactile input at the moving finger shifts attentional resources away from the passive finger, resulting in reduced perceptual sensitivity and attenuated perception of stimuli at that location.

As previously described, *temporal prediction* appears to play a key role in the emergence of sensory attenuation effects. This is evident not only in passive conditions, in which reduced auditory attenuation has been observed for temporally unpredictable stimuli (Schafer & Marcus, 1973; Sowman et al., 2012), but also in self-generated actions when the sensory consequence is temporally delayed or otherwise violated in its expected timing (Blakemore et al., 1999; Kilteni et al., 2019).

Closely related to temporal prediction is the concept of *temporal control*. Temporal control refers to the ability to influence and regulate the timing of actions, events, or processes. It involves coordinating actions in accordance with temporal constraints, task goals, and individual expectations, allowing for flexible adaptation of behavior over time (Aschersleben, 2002). More generally, temporal control is essential for the execution of precise and coordinated movements, as it enables individuals to determine when an action is initiated, how it unfolds over time, and how it is adjusted during execution.

Importantly, Bäß et al. (2008) proposed that temporal control may be even more critical for sensory attenuation than temporal prediction alone. They demonstrated that attenuation effects can occur in situations in which stimuli are temporally controllable, even in the absence of precise temporal predictability. From this perspective, the mere ability to influence the timing of an event may be sufficient to induce attenuation effects. In the context of self-generated actions, temporal control is inherently present, as individuals can determine the onset and structure of their own actions, which in turn contributes naturally to the predictability of their sensory consequences. However, empirical findings suggest that the relationship between temporal control and sensory attenuation is not straightforward. For example, Weiss et al. (2011b) reported that auditory attenuation was stronger when self-generated sounds were produced in response to an external cue compared to completely self-paced actions. This finding indicates that externally provided temporal structure or cueing can enhance attenuation effects, possibly by increasing the precision of temporal predictions. In addition, Harrison et al. (2021) found that reducing temporal control over a stimulus was associated with changes in early sensory processing, as reflected in modulations of the N1 component. Specifically, diminished temporal control led to alterations in N1 amplitude, suggesting that the degree of control over stimulus timing influences early stages of sensory processing and, consequently, attenuation effects.

Another factor closely related to temporal control is the *sense of agency*. The sense of agency refers to the subjective experience of being the initiator of an action (Gallagher, 2000) and includes the feeling of having caused the corresponding sensory consequences of that action (Synofzik et al., 2008). In the context of sensory attenuation, attenuation effects have frequently been used as an implicit measure of agency, based on the assumption that reduced perceptual or neural responses indicate that a stimulus is attributed to oneself (Hughes et al., 2013).

In contrast, explicit measures of sense of agency typically involve direct reports, such as asking participants whether they believe to have caused a particular outcome themselves or to what degree they experienced control over it (e.g., Sato, 2008; Timm et al., 2016). These approaches capture the conscious experience of agency, which may not always align with implicit measures derived from sensory attenuation. The sense of agency has also been investigated using transcranial magnetic stimulation, which can induce movements without voluntary motor commands, thereby allowing a dissociation between movement execution and the sense of agency. Findings from such paradigms suggest that sensory attenuation is reduced or absent when movements are externally induced and lack a corresponding sense of agency (Timm et al., 2014). However, rather than providing definitive evidence that attenuation exclusively depends on self-generated actions, these results are more cautiously interpreted as indicating that the sense of agency contributes to, but may not be solely responsible for, sensory attenuation effects.

With respect to the sense of agency, altered sensory attenuation has also been studied in schizophrenia. Patients with schizophrenia typically show reduced attenuation across multiple modalities, including somatosensory processing and auditory perception of tones (Ford et al., 2014; Whitford et al., 2011), as well as during vocalization, where self-generated speech sounds elicit less suppression compared to healthy individuals (Ford et al., 2007; Ford et al., 2001). These findings are commonly interpreted as reflecting impairments in predictive mechanisms or self-monitoring processes. Supporting this interpretation, pharmacological studies using ketamine to induce schizophrenia-like symptoms in healthy participants have shown comparable reductions in electrophysiological markers such as the N1 suppression during vocalization (e.g., Kort et al., 2017), suggesting a link between altered predictive processing, agency, and sensory attenuation.

In addition to neurophysiological measures, behavioral studies have demonstrated that subjective beliefs about sense of agency can directly influence perceptual outcomes. For example, Desantis et al. (2012) showed that sensory attenuation was modulated by participants' beliefs about authorship, such that tones were perceived as less intense when participants believed they had generated them themselves compared to when they believed the tones had been generated by someone else. This finding highlights the role of higher-level cognitive factors, such as belief and attribution, in shaping sensory attenuation effects.

The relationship between the sense of agency and the P2 component appears to be less consistent. For instance, Weller et al. (2017) reported enhanced P2 amplitudes for delayed tones, suggesting sensitivity of this component to temporal discrepancies rather than sense of agency per se. Moreover, although perceived sense of agency increased under certain delay conditions, P2 amplitudes did not systematically track these changes. In contrast, higher perceived control over sensory outcomes was associated with reduced P2 amplitudes compared to conditions of low perceived control, whereas the N1 component remained largely unaffected. However, given that the functional role of the P2 component in sensory attenuation remains inconsistent and theoretically ambiguous (e.g., Bolt & Loehr, 2021; Crowley & Colrain, 2004; Egan et al., 2023; Klaffehn et al., 2019), the lack of a systematic relationship between P2 amplitudes and sense of agency should be interpreted with caution.

2 Study Summaries

Overall, the role of efference copies and self-generation in the emergence of sensory attenuation is not yet fully understood. Previous studies have reported heterogeneous findings, particularly with respect to attenuation versus enhancement effects (Reznik et al., 2015; Thomas et al., 2022) and the distinction between self- and externally generated stimuli (Han et al., 2021; Han et al., 2022). While the role of temporal prediction has been investigated extensively, its contribution remains inconclusive (Dogge, Hofman, et al., 2019), especially in externally generated contexts. One important source of variability may lie in differences in experimental paradigms and the use of neurophysiological versus behavioral measures (Giannini et al., 2025). Many neurophysiological studies consistently report sensory attenuation in the auditory domain, whereas behavioral studies have shown more variable effects (Korka et al., 2022). For instance, auditory perception of self-generated stimuli has been found to be enhanced at low intensities but attenuated at higher intensities (Reznik et al., 2015). More generally, attenuation effects are often less consistently observed at the behavioral level (Giannini et al., 2025). Similarly, some studies report clear attenuation effects for self-generated touch (Kilteni et al., 2019), others have demonstrated enhanced perception under comparable conditions (e.g., Thomas et al., 2022).

In this dissertation, sensory attenuation was investigated for active and passive movements to determine the role of the efference copy in the auditory and tactile domain. These conditions typically differ in multiple dimensions of predictability, including temporal, proprioceptive, and visual, which need to be disentangled and examined individually in terms of their contribution to attenuation or enhancement effects. In addition, the findings are interpreted in light of attentional mechanisms, as attention may modulate perceptual processing, particularly in multisensory contexts. In this regard, the potential diversion of attention is explicitly addressed, building on previous work of Fritz et al. (2022).

All three studies that were conducted for this dissertation are summarized in this section. Full details are provided in the original research articles and manuscripts, which can be found in the Appendix.

The research question of Study 1 was whether self-generated sounds lead to perceptual attenuation or enhancement, and under which conditions a potential shift between both effects occurs. More specifically, the study examined whether perceptual biases depend on active motor generation itself or can also emerge for externally generated but predictable sounds. Building on findings by Reznik et al. (2015), who reported both effects within the same paradigm, the aim was to examine the origins of these perceptual biases. To this end, all experimental parameters were held constant except for stimulus intensity, which was systematically varied to assess differences in perceptual bias. In addition, the same paradigm was applied to externally generated but temporally predictable tones, as well as to conditions in which participants were adapted to specific volume intensity contexts, in order to assess contextual influences on perceptual bias.

The research question of Study 2 was why predictable or self-generated auditory stimuli produce stronger regression-to-the-mean effects than temporally unpredictable baseline stimuli, and whether attentional mechanisms contribute to this perceptual bias. Specifically, the study investigated whether an increased level of uncertainty and attentional distraction induced by either movement components or additional vibrotactile stimulation modulate the regression pattern observed in Study 1. As this regression effect was only present for self-generated or temporally predictable stimuli, but not in baseline conditions, the aim was to identify the underlying mechanisms driving this pattern. This is particularly relevant given that regression

effects are typically associated with increased uncertainty and reduced perceptual precision, which may be influenced by additional vibrotactile cues during the auditory perception task.

The research question of Study 3 was which factors are critical for sensory attenuation during self-touch, and whether active movement is necessary for attenuation to occur. In particular, the study examined the relative contributions of motor activity, temporal predictability, visual information, and proprioceptive cues to attenuation effects during active and passive self-touch. Movement parameters such as distance, speed, and duration were kept constant to isolate the contribution of motor activity (i.e. presence versus absence of muscle activity). Furthermore, the factors contributing to passive movement conditions were systematically examined. Specifically, predictability was decomposed into visual, temporal, and proprioceptive components, which were individually controlled and manipulated to assess their respective influence on attenuation effects.

All experiments were in accordance with the Declaration of Helsinki and approved by the local ethics committee of the Faculty of Mathematics and Natural Sciences of Heinrich Heine University Düsseldorf. Participants were recruited at Heinrich Heine University Düsseldorf or via social media. Written informed consent was obtained prior to their voluntary participation. Study 1 and 2 were conducted using a DELL OptiPlex 7000 computer and P2419H Screen with a refresh rate of 60 Hz, placed away 57 cm away from the participants. They wore JBL Tune 500 headphones to present tones with a two-alternative-forced-choice (2AFC) task for perceived loudness. In Study 3, a servo motor was used, controlled by an Arduino nano ATmega328 operating at 5 Volt, which moved the right arm of participants towards their left hand and ended in two presented touches conducted by a stepper motor. Again, participants had to judge in a 2AFC task the intensity of stimuli. All experiments were built and run in MATLAB R2021a (MathWorks) using Psychophysics Toolbox v.3 (Brainard, 1997; Kleiner, 2007; Pelli, 1997) or PyCharm 2024.3 (JetBrains, 2024) using Python 3.13 (Python Software Foundation, 2024).

2.1 Study 1: Regression to the mean explains perception of action consequences

The first study has been published as an open-access article in the journal *Proceedings of the Royal Society B* with the following reference:

Johnen, S., & Zimmermann, E. (2025). Regression to the mean explains perception of action consequences. *Proceedings of the Royal Society B: Biological Sciences*, *292*(2057). https://doi.org/10.1098/rspb.2025.1715

2.1.1 Research question and hypotheses

In Study 1, we aimed to address the ongoing debate regarding whether self-generated auditory stimuli lead to perceptual attenuation or enhancement. Competing theoretical accounts have diverging predictions: according to forward model frameworks, self-generated sensory consequences are predicted via efference copies and should therefore be attenuated (e.g., Blakemore et al., 1998; Wolpert et al., 1995). In contrast, other accounts suggest that predicted stimuli may receive enhanced perceptual weighting under certain conditions (e.g., Press et al., 2020; Thomas et al., 2022; Yon et al., 2018; Yon et al., 2021). Notably, Reznik et al. (2015) demonstrated that both, attenuation and enhancement, can occur within the same experiment, depending on stimulus intensity. At the neurophysiological level, sensory attenuation has most consistently been indexed by a reduction in the auditory N1 component (e.g., Ford et al., 2007;

Klaffehn et al., 2019) and P2 component (Bolt & Loehr, 2021; Crowley & Colrain, 2004; Egan et al., 2023; Klaffehn et al., 2019; Timm et al., 2016). However, EEG paradigms might favor the use of clearly audible auditory stimuli to achieve higher signal-to-noise ratios, as reliable ERP estimation depends on sufficiently robust neural responses. As a consequence, previous studies have rarely tested stimuli close to individual hearing thresholds, thereby limiting conclusions about low-intensity perception. To further investigate the conditions under which attenuation versus enhancement occurs, we systematically varied stimulus intensity within the same sample using a behavioral paradigm. This approach allows direct assessment of perceptual biases, which may diverge from neurophysiological markers. Based on the findings reported by Reznik et al. (2015), we hypothesized that self-generated tones would be perceived as enhanced at low intensities and attenuated at higher intensities, thereby reflecting a regression-to-the-mean pattern. Specifically, we aimed to identify the intensity level at which this pattern reverses, with an expected transition around approximately 60 dB, a level commonly encountered in everyday environments like conversational speech (Schandry, 2016).

In addition to self-generated sounds, separate groups of participants performed an identical task with externally generated but temporally predictable tones. This manipulation tests whether temporal prediction alone is sufficient to induce attenuation or enhancement effects (Schafer & Marcus, 1973; Sowman et al., 2012). Finally, to examine the influence of contextual adaptation, participants were exposed to specific volume environments prior to the task. This allowed the investigation of whether perceptual biases shift as a function of recent sensory background. We expected that adaptation would shift the subjective reference level of loudness and modulate the magnitude of enhancement or attenuation, particularly when stimulus intensities deviated from the adapted context and expected volume.

2.1.2 Method

In total, 220 participants (M_{age} = 21.58, SD_{age} = 3.18, 190 female) were tested in four groups, differing in how stimuli were generated: automatically presented with a random delay (baseline), self-triggered (active), or passively generated but cued (continuously or flashed).

Fifty-five participants were tested in the baseline group. Two consecutive tones were presented, and participants had to indicate in a 2AFC task which of the two tones they perceived as louder. Based on their responses, cumulative Gaussian psychometric functions were fitted for each participant and every volume condition to perform to extract PSEs that were used in a repeated-measures analyses of variance (ANOVA) to test for perceived differences.

Each participant completed five volume conditions (40, 50, 60, 70, and 80 dB). Within every volume condition, the first tone, from now on called *probe*, had a fixed intensity corresponding to the respective volume level. The second tone, from now on called *reference*, varied in intensity around the probe level, with seven possible intensities presented in steps of 2 dB. For example, in the 40 dB condition, the probe was always presented at 40 dB, whereas the reference tone ranged from 34 to 46 dB. Each level was presented ten times in randomized order. The order of the volume conditions was randomized across participants, while trials within each condition were presented in blocks. In the baseline condition, participants were not provided with any action instruction or cue predicting the presentation of the probe tone. Instead, the delay between trial onset and probe presentation was randomly jittered between 500 and 3000 ms. The reference tone always followed automatically 500 ms after the probe.

An additional active group (n = 55) completed the same task, with the critical difference that they actively triggered the probe tone. At trial start, participants were instructed to press the space bar to initiate the probe tone. The reference tone again followed automatically after 500 ms. To ensure that the action was experienced as a deliberate movement rather than a minimal habitual key press, participants were instructed to perform a more pronounced movement, moving their hand from the edge of the table towards the space bar every trial.

Two further groups of 55 participants each were tested in passive but temporally predictable conditions designed to match the level of predictability in the active condition. In the first passive group, participants observed two bars located at the left and right edges of the screen, which moved toward each other at a constant speed. When the bars met in the center of the screen, the probe tone was presented. This provided a continuous and fully predictive visual cue for tone onset. In the second passive group, predictability was established via a discrete cue: a fixation cross flashed briefly 700 ms after trial onset, and the probe tone followed 300 ms later. Example trials for all groups are depicted in Figure 1A.

In further groups of Study 1, the influence of contextual adaptation on auditory perception was investigated. Based on the assumption that everyday auditory environments are often centered around moderate sound levels of approximately 60–70 dB (Schandry, 2016), we tested the stability of this presumed perceptual reference. Two additional groups of 55 participants each (M_{age} = 22.16, SD_{age} = 5.67, 88 female) first completed a baseline measurement of 40 and 80 dB trials and were then assigned to a specific context condition. In the loud context group, participants were exposed to tones at 80 dB during an adaptation phase consisting of 70 trials. In the quiet context group, participants were exposed to tones at 40 dB during this phase. In the subsequent test phase, 80 % of trials corresponded to the adapted intensity to maintain the contextual effect, while the remaining 20 % consisted of trials with the opposite intensity, presented in random order. Thus, participants in the loud context group encountered predominantly 80 dB trials, with occasional unexpected 40 dB trials, and vice versa for the quiet context group. Responses to these critical 20 % trials were again used to fit cumulative Gaussian psychometric functions for each participant.

2.1.3 Results and discussion

Deviations between perceived (represented by extracted PSEs) and physically presented sound levels were calculated. Across groups, lower-intensity probe tones tended to be overestimated, whereas higher-intensity tones were underestimated, reflected in negative slopes of the linear fits. This pattern was already present in the baseline condition and is consistent with a regression toward the mean of the stimulus distribution.

In the active group, the slope of this relationship was twice as steep as in the baseline, indicating stronger adaptation to the average sound level. Slopes were used as an index of adaptation strength, revealing significantly higher adaptation in the active compared to the baseline group. A comparable pattern emerged in the temporally predictable passive conditions. Adaptation indices were significantly increased both when the probe tone was cued by a continuous bar and when it was indicated by a flashing fixation cross. Together, these findings suggest that loudness judgments reflect an integration of current sensory input with prior information about the distribution of sound levels. Perception was systematically biased toward the mean of the presented intensities, and this bias increased significantly when the timing of the sounds was cued, as illustrated in Figure 1B. No group differences were observed in JND values, consistent

with findings by Weiss et al. (2011a), who suggested that attenuation primarily reflects a shift in perceptual bias rather than a change in sensory precision, resulting in an intact sensitivity.

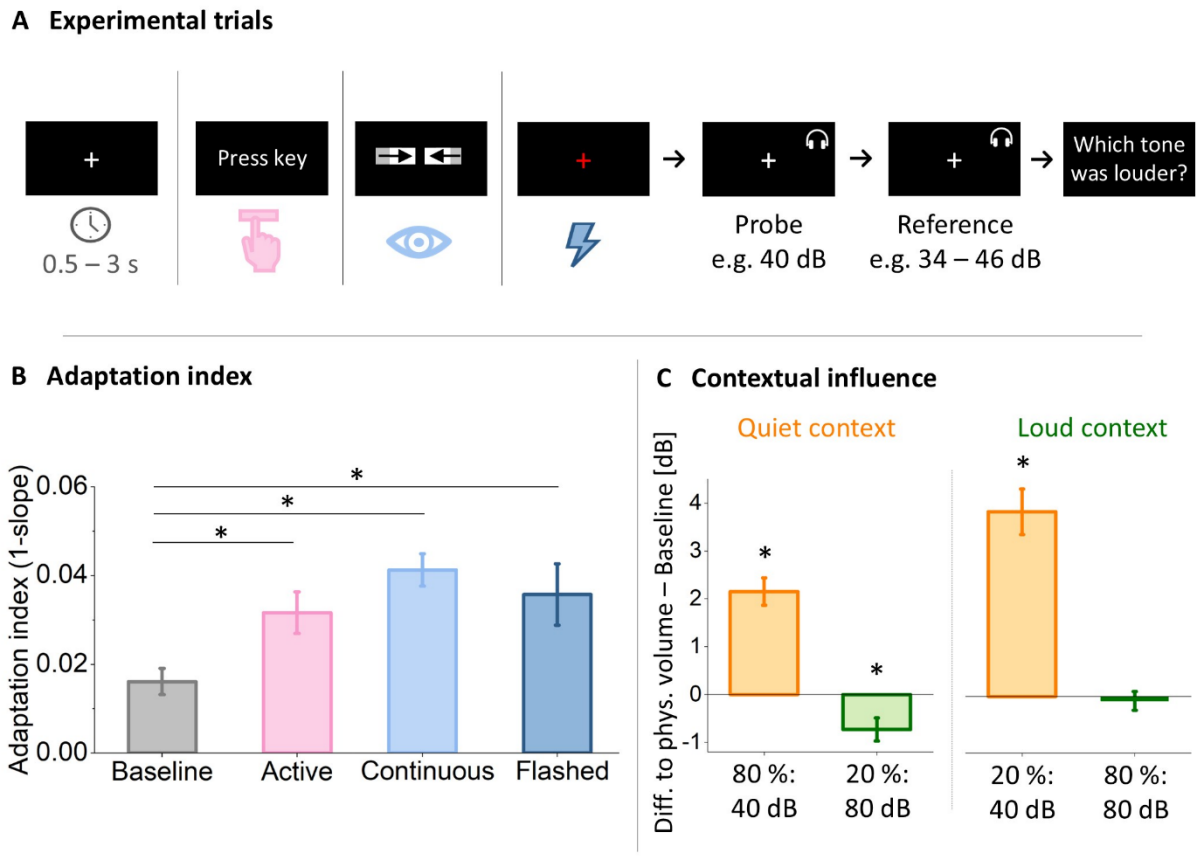
These results provide a unifying perspective on previous findings of both sensory attenuation and enhancement. Rather than reflecting distinct mechanisms, both effects can be understood as consequences of the same underlying process: a shift of perceptual estimates toward the mean sound level. Accordingly, whether a stimulus appears attenuated or enhanced depends on its position relative to the mean.

Importantly, adaptation strength was comparable for self-generated and passively presented sounds when temporal predictability was matched. This pattern is consistent with Bayesian accounts of perception, in which prior expectations bias sensory estimates. Important to note is that a match between prior expectations and the actual sensory outcome might lead to neurally reduced ERPs while being perceived perceptually as either enhanced or attenuated, depending on the circumstances (Press et al., 2020). The results indicate a regression to the mean as a function of the presented sound intensity. At the same time, it challenges forward model accounts that assume a general attenuation mechanism for self-generated input (Hughes et al., 2013). In particular, such models do not readily explain the enhancement effects observed here, which occurred across a broad range of intensities, whereas attenuation was largely restricted to higher sound levels.

Additional investigations manipulating sound-level context further support a role of statistical adaptation. Loud tones presented in a loud context were perceived similarly to baseline, but appeared attenuated in a quiet context. Conversely, quiet tones were perceived as louder when embedded in a loud context, with substantial shifts in perceived intensity (see Figure 1C). These context-dependent effects indicate that perceptual estimates are dynamically adjusted based on recent stimulus statistics. This interpretation is in line with neurophysiological evidence showing that auditory neurons adapt rapidly to changes in mean sound level, with time constants on the order of 160 ms (Dean et al., 2005). The present behavioral results suggest that temporal predictions, whether arising from self-generated actions or external cues, facilitate this adaptive process.

Notably, enhancement effects were generally more pronounced than attenuation effects, particularly in loud contexts. Interestingly, this asymmetry appears to contrast with previous auditory physiology findings suggesting faster neural adaptation to increases than to decreases in sound level (e.g., Dean et al., 2008). In summary, the present findings indicate that perception of sound intensity is shaped by contextual regularities in the environment and their temporal predictability. The results support an account based on adaptive, prediction-driven processing of sensory input, without requiring a mechanism specific to self-generated actions.

Figure 1: Experimental trials and results of Study 1



Note. **A)** shows an example trial for the four tested groups. **B)** shows the slope strength for the according groups. **C)** shows the differences of the perceived to the physically presented volume in relation to the baseline for the quiet as well as the loud context group. Asterisks indicate $p < .05$.

2.2 Study 2: Cross-Modal Interference Explains Perceptual Biases for Action Consequences

The second study is currently submitted as open-access article:

Johnen, S. & Zimmermann, E. (2026). Cross-Modal Interference Explains Perceptual Biases for Action Consequences. *Psychological Science - Submitted*.

2.2.1 Research question and hypotheses

In Study 2, the regression pattern reported in Study 1 was examined regarding its origins. As previously reported, participants showed enhanced perception of quiet tones and attenuated perception of loud tones, reflecting an adaptation toward the mean sound level. This regression pattern was present for both self-generated and externally generated but temporally predictable tones. Study 2 aimed to clarify whether this regression pattern is primarily driven by predictability, accounting for the similarly strong effects across self-generated and externally predictable conditions, or by a diversion of attention induced by actions or additional cues, which may reduce

perceptual precision (Fritz et al., 2022). Since the effect was present only in temporally predictable conditions, the question arose why the improved prediction of an auditory stimulus leads to a stronger perceptual regression to the mean.

Classic research on sensory attenuation has mainly focused on the role of movement and motor planning (e.g., Blakemore et al., 1998; Kilteni et al., 2018; Kilteni et al., 2020). However, such paradigms are often confounded by concurrent sensory signals, such as visual and tactile feedback during actions (e.g., moving the hand toward a button), which may draw attention away from the sensory consequences of the action. The role of attentional diversion has been demonstrated by Fritz et al. (2022), who showed that tactile feedback in the acting hand appears to be necessary for attenuation effects at a passive finger. They argued that processing tactile input at the moving finger shifts attentional resources away from the passive finger, resulting in reduced perceptual sensitivity to stimuli at that location.

In line with this account, Saupe et al. (2013) explained typical neural signatures of sensory attenuation, such as N1 suppression, in terms of attentional modulation. Specifically, N1 suppression was reduced or absent when participants attended to auditory stimuli, but emerged when attention was directed away from them. Similar conclusions were drawn by SanMiguel et al. (2013) who interpreted attenuation as a consequence of a reduced attention-related orienting response. Because self-generated sounds are less surprising, they attract less attention, which in turn leads to a reduced perceived intensity.

Jones et al. (2013) investigated the interaction between attention and predictability and found that directing attention to sounds reduced attenuation effects, even for predictable, self-generated stimuli. Conversely, the strongest attenuation was observed when stimuli were both predictable and unattended. Converging evidence comes from Kok et al. (2012), who demonstrated that predicted stimuli elicited reduced neural responses when unattended, whereas attended predicted stimuli showed enhanced neural processing. Their findings suggest that attention increases the precision or gain of sensory signals, thereby modulating predictive processing. Similar conclusions were reported by Harrison et al. (2021), who proposed that sensory attenuation reflects an interaction between prediction and attention rather than prediction alone.

In Study 2, the aim was to disentangle the underlying components by systematically isolating movement, prediction, and tactile feedback in order to differentiate between prediction- and attention-based accounts. In addition, we investigate how different sources of predictability and attentional diversion contribute to regression to the mean in auditory perception. We hypothesize that the characteristic regression pattern (enhancement of quiet and attenuation of loud tones) will be most pronounced in conditions that induce the strongest diversion of attention.

2.2.2 Methods

In total, 220 participants were included in the analysis (M_{age} = 22.55, SD_{age} = 3.72, 164 female). The sample size was chosen to match that of each group of Johnen and Zimmermann (2025), in which regression effects were found as a function of sound-level presentation. Participants were randomly and equally assigned to one of four groups. In addition to the setup previously described in the beginning of section 2, a motion tracker (Ultraleap Stereo IR 170) was positioned 45 cm from the table edge.

In the baseline group, participants judged which of two tones was louder. After trial onset, the probe tone was presented following a random interval between 500 and 3000 ms, identical to the baseline procedure used in Johnen and Zimmermann (2025). The reference tone was presented 500 ms later. Probe tones were presented at one of five possible sound levels (40, 50, 60, 70, or 80 dB) on each trial. Each probe level was presented in blocks, with block order randomized across participants. For each probe level, the reference tone was selected from seven possible sound levels, symmetrically centered around the probe level with a step size of 2 dB. For example, in the 80 dB condition, the reference tone could take values of 74, 76, 78, 80, 82, 84, or 86 dB. Each reference level was presented ten times in randomized order, resulting in a total of 350 trials per session. After presentation of the reference tone, participants responded by pressing the left or right arrow key to indicate which tone they perceived as louder.

In the vibro-tactile group, the loudness judgment task was identical to the baseline group. In addition, participants received a vibro-tactile stimulus (Vibrocoin ERM motor, controlled by an Arduino Nano microcontroller, ATmega328, operating at 5 V) on the right index finger, presented simultaneously with the tone. As in the baseline condition, a random delay of 500 to 3000 ms was used in each trial to render the onset of both tone and vibration unpredictable.

In the motion group, participants were instructed to trigger the probe tone themselves. To do so, they performed a reaching movement above a detection sensor, which triggered the probe tone as soon as the hand passed the sensor. The reference tone followed automatically after 500 ms. No tactile feedback was provided at the movement endpoint.

The motion–vibration group performed the same reaching movement as the motion group. In addition, a vibro-tactile stimulator was attached to the index finger, delivering a vibration simultaneously with the probe tone when the sensor was triggered. This condition approximates a typical self-generated paradigm in which participants press a button to elicit a tone, combining both movement and tactile feedback. Example trials for all groups are depicted in Figure 2A.

In a further experiment of Study 2, we investigated whether different levels of attentional diversion lead to differences in regression strength. All 165 participants (M_{age} = 23.58, SD_{age} = 6.15, 131 female) performed the same task as the vibro-tactile group from the previous experiment. Three levels of vibro-tactile intensity were implemented in a between-subjects design to manipulate the degree of distraction. The strongest vibro-tactile group received the same stimulation as in the previous experiment (average intensity: 5 V), the medium group received 50 % of that intensity (2.5 V), and the low-intensity group received 25 % (1.25 V), while ensuring that this level remained above individual perception thresholds.

Afterward, participants in all three groups completed the same auditory 2AFC discrimination task with probe levels between 40 and 80 dB and corresponding reference levels at seven intensities symmetrically distributed around the probe. Deviations of the PSEs from the physically presented sound levels served as an index of perceptual bias. No movement was required; tones and vibrations were presented after a random delay of 500 to 3000 ms following trial onset, without any additional temporal cues. All conditions and groups were analyzed by using the deviations of the PSE to the physically presented volume to and then compared in a repeated-measured ANOVA including the group as between-subject factor. In addition, linear regressions were fit for every participant and afterwards again compared using a repeated-measures ANOVA with the between-subject factor group.

2.2.3 Results and discussion

In general, quiet tones (40 to 60 dB) were perceived as louder, whereas loud tones (80 dB) were perceived as less intense, reflecting a regression toward the mean sound level. The strength of this effect varied depending on the group to which participants were assigned. Following the analysis of Johnen and Zimmermann (2025) in Study 1, linear regressions of the first experiment were fitted for each participant across sound levels from 40 to 80 dB, and the resulting slopes were used as an index of adaptation strength. All experimental groups, the vibro-tactile, motion, and motion–vibration groups, showed significantly steeper slopes than the baseline group, but did not differ significantly from one another (see Figure 2B). This pattern indicates that prediction alone is not necessary to produce regression to the mean.

In the vibro-tactile group, vibrations were presented simultaneously with the probe tone after a random delay, and this condition showed significantly stronger regression than the baseline group. As the only difference between the vibro-tactile and baseline groups was the presence of the vibration, this finding suggests that attentional diversion plays a critical role in shaping the regression pattern. At the same time, predictive cues, especially when presented in a modality different from the target stimulus, may also act as sources of attentional diversion. The motion–vibration group served as a comparison to classical self-generated tone paradigms, as it combined self-initiated movement with tactile feedback, comparable to a button press. This replication was successful, as the same regression pattern was observed and differed significantly from the baseline condition.

We aimed to disentangle the components typically involved in classical attenuation paradigms using button presses. Study 1 demonstrated that regression occurs both for self-generated and externally generated but predictable stimuli. In the present study, we examined why predictability leads to regression toward the mean and found that attentional diversion appears to play a central role. Decomposing a button press reveals several contributing factors, including movement, prediction, control, and tactile feedback. Our results suggest that temporal predictability alone cannot account for all found regression effects, as regression was also observed in temporally unpredictable conditions that involved attentional diversion. Notably, there were no significant differences between a predictable, self-generated movement triggering a tone and a randomly presented tone paired with a vibro-tactile stimulus.

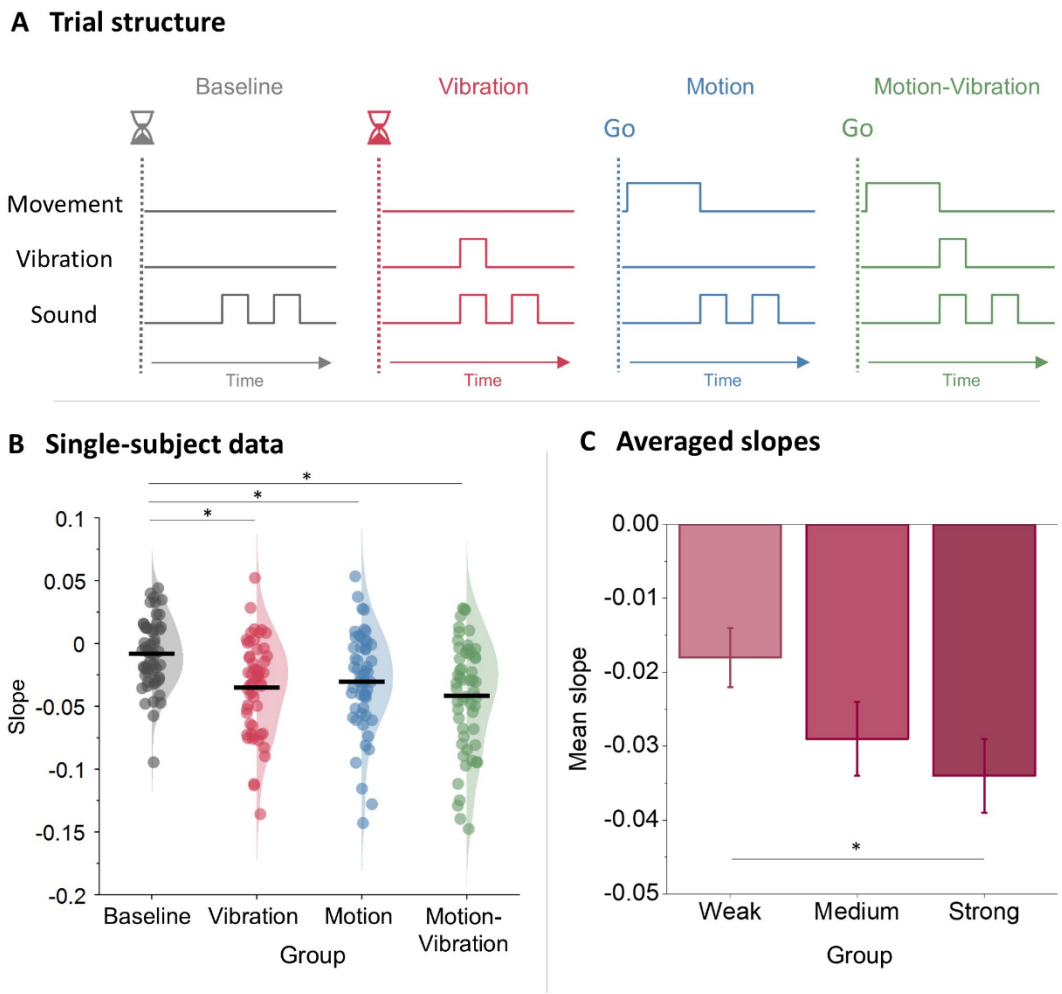
In addition, we included a motion-only group that lacked tactile feedback. According to Fritz et al. (2022), sensory attenuation is only observed when tactile feedback accompanies the stimulus. However, we still observed regression effects for auditory stimuli following movement without tactile input. Different to Fritz et al. (2022), we analyzed the full range of sound levels rather than focusing on a single intensity (62.3 dB), which may explain why we did not replicate their findings under those conditions. Overall, regression was observed in both predictable conditions (motion and motion–vibration) and in the unpredictable but attentionally diverted vibro-tactile condition, indicating a certain level of robustness of the regression effect while informing the distinction between prediction and attentional diversion.

In the second experiment of Study 2, the negative regression slope got stronger with increasing vibro-tactile stimulation and was significantly steeper in the strong- compared to the low-intensity group (see Figure 2C). This indicates that stronger attentional diversion leads to a greater reliance on regression toward the mean. To examine whether attentional diversion follows a graded pattern, a linear function was fitted to the regression slopes across all three groups and revealed a significant linear trend, indicating that increasing vibration intensity led to steeper

regression slopes and thus stronger perceptual bias in the auditory domain. Steeper slopes therefore reflect a greater influence of the concurrent tactile signal on auditory judgments, suggesting that the weighting of sensory information shifts as a function of stimulus intensity. This pattern can be interpreted as evidence for a graded allocation of attentional resources: stronger tactile stimulation captures more attention, thereby reducing the resources available for auditory processing. As a consequence, auditory judgments become less precise and rely more strongly on prior expectations, resulting in steeper regression slopes (cf. Jazayeri & Shadlen, 2010).

In Study 2, we examined why prediction of auditory stimuli, either through self-generation or external cues, leads to less precise perception, as reflected in regression patterns. The results of the vibro-tactile condition demonstrate that predictability alone is not sufficient to explain all effects; rather, attentional diversion appears to be the critical factor. This interpretation is further supported by the second experiment, in which systematically increasing levels of vibro-tactile distraction during tone presentation led to progressively steeper regression slopes. The stronger the distraction, the stronger the regression toward the mean.

Figure 2: Trial structure and results of Study 2



Note. **A)** illustrates a single trial example of each group. **B)** shows a raincloud plot of the four groups of Experiment 1. **C)** depicts the slopes from Experiment 2, sorted by vibration strength. Asterisks mark significant differences with $p < .05$.

2.3 Study 3: Sensory attenuation reflects proprioceptive recalibration rather than motor forward models

The third study has been submitted for publication as an open-access article:

Johnen, S., Bayer, M., & Zimmermann, E. (2026). Sensory attenuation reflects proprioceptive recalibration rather than motor forward. *iScience – Under Review*.

2.3.1 Research question and hypotheses

In Study 3, we further investigated whether sensory attenuation is primarily driven by active stimulus generation or by predictive processes, focusing on tactile information. While audition primarily signals events at a distance, touch provides information about direct contact with the body. For decades, research has shown that self-generated touch is perceived as less intense than externally generated touch of comparable physical intensity (Bays et al., 2006; Bays et al., 2005; Blakemore et al., 1999).

Two main theoretical frameworks have been proposed to explain sensory attenuation in this context. Forward model accounts assume that an efference copy of the motor command is used to predict the sensory consequences of an action (e.g., Kawato, 1999; Wolpert et al., 1998). If the actual sensory input matches these spatiotemporal predictions, the resulting sensation is attenuated (e.g., Bays & Wolpert, 2008; Job & Kilteni, 2023). However, accumulating evidence suggests that attenuation may not depend on self-generation per se, but rather on the predictability of sensory events (Dogge, Custers, et al., 2019; Press & Yon, 2019). Supporting this view, Bays et al. (2005) demonstrated that attenuation is not restricted to the sensation of an active movement, but also requires that the sensory consequences at the receiving body part are predictable. Even the expectation that one's arm will be moved can reduce the perceived intensity of subsequent tactile input (Voss et al., 2008). Furthermore, attenuation decreases when the spatial relationship between action and sensation is disrupted, for example when the distance between the touching and touched finger exceeds approximately 10 cm or when spatial congruency between movement and tactile consequence is reduced (Bays & Wolpert, 2008; Knoetsch & Zimmermann, 2021).

An alternative account is provided by active inference, which reverses the functional hierarchy assumed in forward model accounts (Adams et al., 2013). In this framework, proprioceptive predictions about a desired future state of the body drive movement by minimizing the discrepancy between predicted and actual states. Sensory attenuation is thought to arise from a reduction in the precision of sensory input, allowing these predictions to guide action (Brown et al., 2013).

Self-touch represents a particularly informative case for distinguishing between these frameworks. In motor control theories as forward models, attenuation arises from predictions based on efference copies in the acting limb (Blakemore et al., 1998). In contrast, active inference allows for predictions not only in the moving limb but also at the expected site of contact, as part of selecting a somatosensory target on the body (Brown et al., 2013). Thus, the key difference between the two accounts lies in whether predictions are derived from motor commands or from higher-level inferential processes that precede movement planning (Adams et al., 2013).

In the present study, we tested these competing accounts by systematically examining the role of predictive cues in a self-touch paradigm. Previous work has shown that sensory attenuation is sensitive to the spatial and temporal structure of actions. However, explaining attenuation solely

in terms of forward models implies a tight coupling between prediction error and perceived intensity, an assumption that has been questioned both theoretically and empirically. In contrast, several studies suggest that Bayesian models, in which perception reflects a combination of sensory input and prior expectations, may provide a more comprehensive account of attenuation effects (Huang & Rao, 2011). An open question concerns the role of passive movements that are self-initiated, self-controlled, or otherwise predictable. Specifically, it remains unclear whether attenuation depends on the distinction between self-generated and externally generated actions, or more generally on the ability to anticipate upcoming sensory events.

Another important factor is the role of contact between the active and passive hand. In many paradigms, the movement of the active hand directly triggers tactile stimulation on the passive hand, creating a clear causal link. When no physical contact occurs, this causal relationship is absent. However, previous findings suggest that attenuation can still arise if contact is expected, even when it does not occur (Bays et al., 2006). This was further supported by Job and Kilteni (2023), who showed that self-generated touch is robustly attenuated regardless of whether the two hands make contact, as long as the contact was expected. When participants expected to touch their own hand, attenuation occurred even if the contact was unexpectedly missed. In addition to causal and spatial relationships between the acting and receiving hand (Bays & Wolpert, 2008; Knoetsch & Zimmermann, 2021), it has also been suggested that movements need to be voluntary and based on natural action–outcome associations rather than arbitrary mappings (Kilteni & Ehrsson, 2022; Kilteni et al., 2020). For example, in a passive condition in which the acting hand simply fell onto a sensor that triggered stimulation on the other hand, no attenuation was observed despite the movement being self-generated (Kilteni et al., 2020). This idea is further supported by recent studies suggesting that predictive mechanisms are specifically tuned to the expected sensory consequences of goal-directed actions rather than to movement execution itself. Fuehrer et al. (2022), for example, demonstrated that tactile suppression was strongest when externally presented tactile probes matched the predicted sensory feedback associated with a movement across a specific texture. Thus, attenuation-related effects may depend less on movement per se than on the extent to which a specific sensory outcome is anticipated.

To disentangle the contributions of different predictive signals, we systematically isolated their effects on sensory attenuation during self-touch. We developed an experimental setup that allowed us to closely mimic self-generated movements of the right hand leading to tactile stimulation of the left hand. In this setup, one motor passively transported the participant's right arm, while a second motor delivered a tactile stimulus to the left index finger when the arm reached a predefined position. This design enabled us to separate movement-related from prediction-related influences on perception. We hypothesized that if predictability is the critical factor, passive movements that are equally predictable as active movements should produce comparable levels of attenuation.

In a second step, we further examined specific sources of predictability in passive conditions. Several cues could allow participants to anticipate the occurrence of the tactile stimulus. First, visual information about the moving hand could provide predictive information about the upcoming touch. Second, the temporal structure of the movement, determined either by active execution or passively by the constant speed and distance of the motor, could support precise temporal expectations. Third, proprioceptive signals arising from the movement of the arm, whether self-generated or externally induced, could inform participants about the timing of the expected contact. These components were investigated individually to determine their respective contributions to sensory attenuation.

2.3.2 Method

In total, 59 participants took part in the first experiment, of whom 55 (M_{age} = 28.42, SD_{age} = 12.14, 39 female) were included in the analyses. We studied the perceived intensity of tactile stimuli during self-touch. The experimental apparatus was custom-built to investigate tactile perception and consisted of a rigid chassis originally designed as a printer frame. The chassis provided a linear guide system along which a movable platform (hereafter referred to as the carrier) could be precisely translated. The carrier was mounted on the chassis and driven by a stepper motor, allowing controlled linear movement along a single axis. Motor control enabled smooth and repeatable positioning of the carrier with high spatial precision. The carrier served as an arm support on which participants rested their right forearm in a stable posture. During the experiment, the right index finger was extended and oriented in the direction of movement. The carrier advanced along the chassis until the participant's right index finger touched a vertically mounted metal plate positioned at a fixed location along the movement path. Behind the metal plate, the participant's left hand was secured using a Velcro fastener such that the left index finger was aligned with the contact location of the right index finger (Figure 3A). The mechanical design ensured reproducible movement trajectories and consistent timing of tactile events across trials and participants, making the apparatus suitable for controlled investigations of tactile perception.

In a separately measured baseline of 20 trials, participants were instructed to rest their right arm on the carrier such that their right index finger touched the metal plate. During the baseline, the right arm remained stationary. Tactile stimuli were applied to the participants' left index finger after a random delay between 500 and 3000 ms using a small wooden rod. The rod was attached to a servo motor and controlled by an Arduino Nano ATmega328. The interval between the first and second touch was fixed at 1000 ms. Participants then performed a 2AFC task using a USB triple foot switch, indicating which of the two touches they perceived as stronger. A 20-trial adaptive Robbins–Monro procedure, operating between 0.5 and 3.5 N, was used to estimate the sensory threshold for each participant and condition. The intensity of the first touch (probe) remained constant at 2 N, whereas the intensity of the second touch (reference) was adjusted depending on the participant's responses on a foot pedal.

In the self-generated experiment, participants were instructed to move their right arm on the carrier back and forth along the rail until they heard a signal tone, which marked the reversal position. An HTC Tracker (3.0) was mounted on a wooden carrier to record the position of the right arm using. At the beginning of the session, several calibration trials were conducted to determine the exact touch position and an additional position located 5 cm away as well as to familiarize themselves with the setup and required movement. A virtual environment was implemented using Unreal Engine (version 4.26). Tracking was implemented using SteamVR (version 1.25.3) and the SteamVR 2.0 tracking system. Threshold estimates were defined as the intensity levels reached by the adaptive staircase procedure in the final trial of each of the six blocks. The movement distance of 5 cm remained constant throughout.

In the indirectly generated condition, the movement was executed by the stepper motor but controlled by the participants via the middle foot pedal. Participants were instructed neither to resist nor assist the movement. The right arm was moved on the carrier back and forth along the rail by a stepper motor, controlled by a separate Arduino Nano ATmega328.

After testing the indirectly generated condition, we next examined the role of motor control. In the following experiment, participants (M_{age} = 22.24, SD_{age} = 2.63, 46 female) no longer controlled the stepper motor; instead, it was operated by the experimenter. The experimenter initiated the movement by pressing a key that was not visible for the participants. The remaining procedure was identical to the indirectly generated condition. Additionally, the indirect condition was repeated with participants blindfolded, using the same sample of participants as in the externally controlled experiment.

In a separate group of participants, the influence of movement speed and distance was investigated by introducing a short-fast condition (0.5 cm distance at 3 cm/s). The externally generated condition served as a long-slow condition (5 cm distance at 1 cm/s). Psychometric functions were estimated using constant stimuli with nine reference levels (ranging from 1.6 to 2.4 N in equiprobable steps), resulting in a total of 360 trials. The reference levels were symmetrically distributed around the probe level of 2 N, with step sizes increasing toward the extremes (0.025, 0.175, and 0.375 N). All 55 participants (M_{age} = 23.17, SD_{age} = 3.95, 48 female) additionally completed an independent baseline measurement without movement. The same sample also performed a recalibration condition, in which the arm was moved 5 cm backward at 1 cm/s to recalibrate the self-touch position. The first touch was delivered when participants reached the reversal point of the movement, which served as the recalibration point. In subsequent experiments, virtual reality equipment was no longer used for tracking.

To investigate the role of proprioceptive prediction, another sample of 55 participants was tested (M_{age} = 23.17, SD_{age} = 3.95, 48 female). In addition to a baseline measurement, the right arm was moved forward and backward with four possible touch positions. Tactile stimuli were delivered either during forward movement, during backward movement, at the reversal point, or at the original self-touch position. At trial onset, no cue was provided to indicate when the touch would occur. The same sample also completed a visual spatiotemporal predictability experiment. In this condition, the right arm remained stationary. Instead, a segment of a standard SMD LED strip was positioned either 0.5 cm behind the touched finger (congruent condition) or 60 cm away from the participant, 42 cm from the carrier, and 55 cm from the touched finger (incongruent condition). One of the two LEDs illuminated randomly and cued the tactile stimulus, which was delivered 500 ms later.

2.3.3 Results and discussion

A significantly attenuated perception of actively self-generated touch was found compared to a non-moving baseline. The analysis further revealed a significant effect of time, with increasing attenuation and larger deviations from baseline across trials. Consistent with this pattern, movement speed also increased over time, suggesting that participants became more familiar with the setup and executed their movements in a more natural manner (Figure 3B).

Similar to the self-generated condition, all estimates in the indirectly generated experiment were negative, indicating reduced perceived intensity of the touch. In contrast to the active condition, no significant effects of time or movement speed were observed, as movement was controlled by the motor. The average attenuation in the indirectly generated condition differed significantly from baseline. Moreover, there was moderate evidence for the absence of a difference between self-generated and indirectly generated movements. This finding suggests that self-generation is not a necessary factor for sensory attenuation, as the effect was equally strong in indirectly and

externally generated conditions. Consequently, a forward model based solely on efference copy signals is unlikely to fully account for the observed effects.

Further analysis of movement speed showed that a shorter and faster movement produced attenuation comparable to that observed for the longer and slower movement. Both conditions resulted in significantly attenuated touch perception compared to the baseline (Figure 3C).

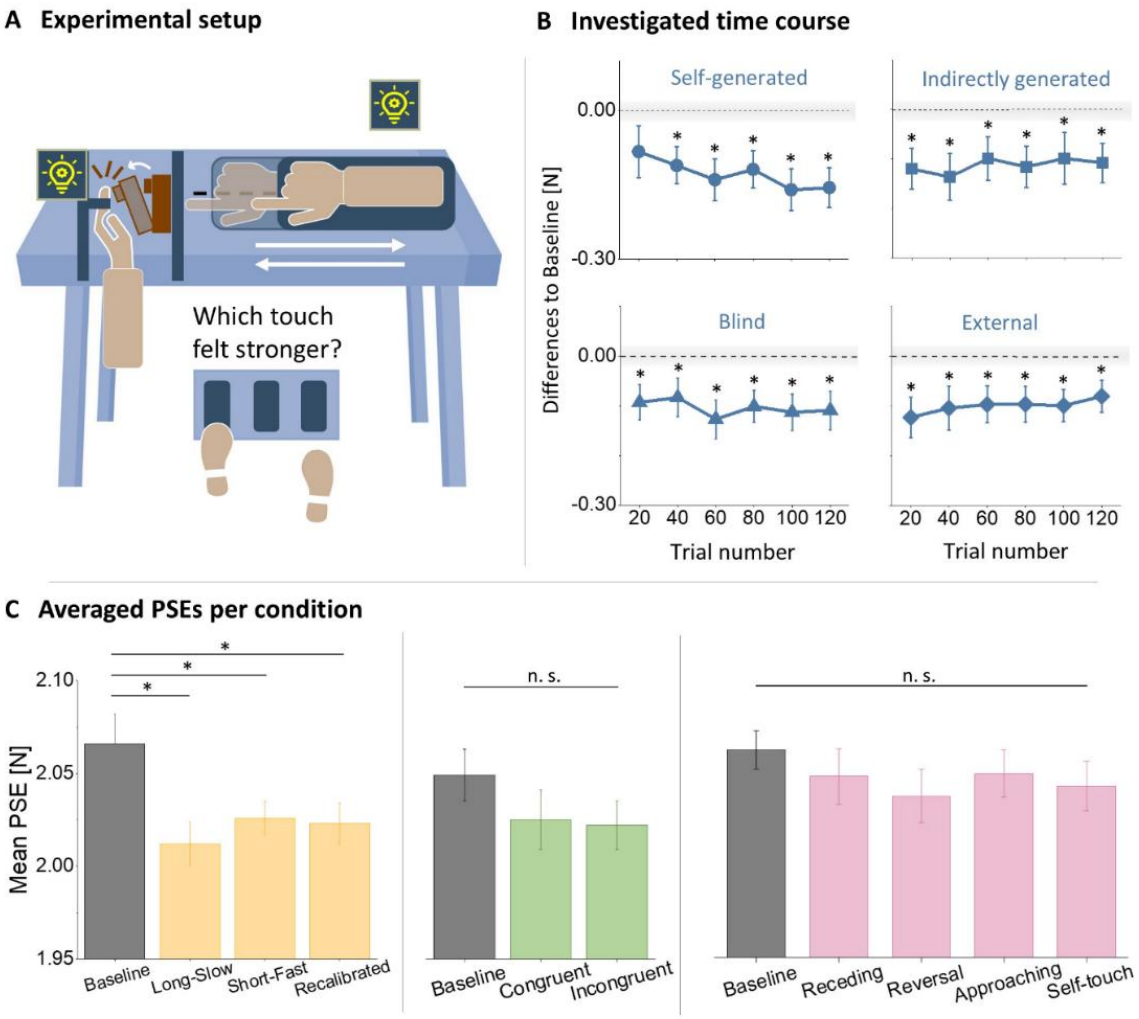
In addition to movement speed, movement control was examined. In the indirectly generated condition, participants retained some control over the motor, which was removed in the externally generated condition. Nevertheless, attenuation remained present compared to baseline and was comparable in magnitude to the indirectly generated condition, again with moderate evidence supporting similarity. The timing of measurement had no effect. The same result pattern applies to the blindfolded condition.

To examine the contribution of different aspects of predictability, visual and temporal predictability were investigated next. No differences were found between congruent and incongruent target positions or relative to a neutral baseline condition. When testing the necessity of visual information, attenuation was still observed in the absence of vision, comparable to the indirectly generated condition. Similarly, temporal predictability did not affect attenuation in an LED-cued experiment. Together, these findings indicate that neither visual nor temporal predictability alone is sufficient to account for the effect.

When proprioceptive predictability was removed by presenting stimuli at random positions, attenuation disappeared and was no longer distinguishable from baseline. This suggests that proprioceptive predictability is a critical factor in tactile sensory attenuation. In this condition, the position of the right arm at the time of stimulation was randomized, preventing reliable predictions prior to each trial. However, after recalibrating the self-touch position, attenuation re-emerged. This effect was reduced in magnitude but remained significantly different from baseline. It is possible that a greater number of trials or a longer exposure phase would strengthen this recalibrated association. This interpretation is consistent with previous findings from the rubber hand illusion, which demonstrate that perceived hand position can be recalibrated even in the absence of visual input (Aimola Davies et al., 2013; Ehrsson et al., 2005; White et al., 2011).

In Study 3, we systematically examined the factors contributing to sensory attenuation in the tactile domain. The experimental setup allowed us to keep general conditions constant while selectively manipulating individual components to identify necessary and sufficient factors. Overall, the results are neither consistent with active inference accounts nor with forward model approaches that assume a critical role for efference copies. Within active inference frameworks, sensory attenuation is proposed to arise from a temporary reduction in the precision weighting of sensory evidence during movement, allowing proprioceptive predictions to guide action execution (Brown et al., 2013). The presence of comparable attenuation effects during passive predictable movement appears difficult to reconcile with the assumption that attenuation primarily serves the implementation of self-generated actions.

Figure 3: Experimental setup and results of Study 3



Note. **A)** shows experimental setup. Participants rested their right arm on a platform that moved depending on the according condition. Touches were applied to the left index finger. LEDs lit up in the visual spatiotemporal condition. **B)** illustrates results of all conditions including time course measurements. **C)** includes averaged PSEs for remaining conditions. Asterisks indicate $p < .05$, n. s. = not significant.

3 General Discussion

This dissertation primarily investigated whether sensory attenuation is a consequence of self-generation or prediction in the auditory and tactile domain. Since previous studies have shown that the forward model account is partly insufficient and cannot fully explain the causes and different manifestations of attenuation (Dogge, Custers, et al., 2019), the present work aimed to systematically disentangle the contributing factors. In both the auditory and tactile domains, all parameters were kept identical between self-generated and externally generated conditions to ensure comparability.

In the auditory domain (Study 1), the only difference between the active, flashed, and continuously cued conditions was the type of prediction involved. In the self-generated condition, participants pressed the space bar to trigger the first tone, which represents the classical procedure in auditory sensory attenuation paradigms that have been used similarly before (Sato, 2008; Weiss et al., 2011a). By introducing externally generated but temporally predictable stimuli, the motor component was removed while stimulus properties remained identical across conditions.

In Study 2, the mechanisms underlying the regression to the mean effects observed in Study 1 were examined more closely. Since regression effects were found in both self-generated and externally cued conditions, the question arose why the mere presence of predictive cues would induce such a bias toward the mean. Typically, regression to the mean is interpreted as a consequence of uncertainty in perceptual estimates (Jazayeri & Shadlen, 2010; Murai & Yotsumoto, 2018; Petzschner et al., 2015; Zimmermann & Cicchini, 2020), which appears paradoxical given that predictability was increased in these conditions. Therefore, Study 2 investigated the potentially distracting effects of predictive cues by isolating different components of self-generated tones and disentangling their respective predictive and attentional contributions.

The same logic was applied in Study 3 in the tactile domain, where all movement parameters, such as distance, direction, speed, and, critically, the timing of the sensory outcome, were tightly controlled. In the first experiment of Study 3, all these parameters were identical except for the source of movement generation: in one condition, participants actively moved their arm, whereas in the other, their arm was passively transported by a carrier. As this manipulation resulted in comparable levels of tactile attenuation, subsequent experiments systematically investigated additional components of movement and prediction in the context of self-touch in a stepwise manner.

Across the three main studies, a consistent pattern emerged: sensory attenuation occurred to a comparable extent in both self-generated and externally generated conditions, provided that the stimuli were predictable or combined with additional stimuli. Importantly, these findings are not in line the classical forward model account, which depends on the presence of an action. Moreover, forward model-based theories cannot readily explain enhancement and regression effects, as they have been found for quiet tones. These findings suggest that sensory attenuation and enhancement may reflect two manifestations of the same underlying mechanism; an adaptation toward the mean sound level. However, predictive cues might be associated with a diversion of attention away from the auditory task. Thus, prediction alone may also be insufficient to fully account for sensory attenuation, or more precisely, for regression-to-the-mean effects. In the following, these findings are integrated and discussed in relation to existing theoretical accounts, with a particular focus on their implications for forward model theory.

3.1 Enhancement versus attenuation

The present findings raise a fundamental question regarding the origin of sensory attenuation itself. Specifically, it remains unclear whether self-generated sensations are generally attenuated, or whether the observed effects reflect a more complex, context-dependent perceived intensity.

In the present studies, perceived intensity was systematically overestimated for low-intensity stimuli and underestimated for high-intensity stimuli, indicating a bidirectional effect rather than a uniform attenuation. This pattern is consistent with an adaptation toward the mean of the sensory context following a regression pattern. Given that the human auditory system operates over a wide dynamic range but exhibits its highest discriminability within a comparatively narrow intensity window, perceptual sensitivity appears to be dynamically adjusted to the statistical properties of the environment. Human loudness processing spans a range of approximately 120–140 dB. However, the effective range within which fine discrimination occurs is much narrower, typically around 30–40 dB (Dean et al., 2005; Viemeister, 1988). To cover the full dynamic range, this sensitive operating window might shift toward the mean sound level of the current context. As a consequence, stimuli below the contextual mean are perceptually enhanced, whereas stimuli above the mean are attenuated, turning sensory attenuation and enhancement into expressions of a regression pattern.

Next to the dynamic shift explanation, another possibility regarding the regression-to-the-mean pattern relates to the comparison task itself. Participants were required to compare a probe tone with a similar automatically presented reference tone, a procedure that may have already increased perceptual uncertainty and reduced discriminability. Psychophysical research has shown that under conditions of increased uncertainty or difficult magnitude judgments, participants tend to rely more strongly on central or average responses, resulting in regression-to-the-mean or centering effects (Jazayeri & Shadlen, 2010; Poulton, 1979; Stevens, 1957). Regression to the mean effects have, for example, been previously observed in time reproduction tasks, suggesting that the brain incorporates knowledge about temporal uncertainty to adapt internal timing mechanisms to the temporal statistics of the environment (Jazayeri & Shadlen, 2010; Murai & Yotsumoto, 2018; Zimmermann & Cicchini, 2020). Increased uncertainty is associated with an increased tendency toward regression to the mean (Murai & Yotsumoto, 2018). Within the present paradigm, such a mechanism could have biased participants towards the according mean when sensory judgments became less reliable. Consistent with this idea, regression was already observed in the baseline but significantly flatter than in experimental groups. Importantly, however, the explanation of a demanding comparison task alone appears insufficient to account for the present findings. The comparison task itself was identical across all groups, including the temporally unpredictable baseline group as well as passive and active groups, but led to significantly different regression slopes. The addition of actions or external stimuli may have increased uncertainty, leading participants to rely more strongly on prior expectations and consequently resulting in a stronger regression effect. This suggests that the regression pattern was not merely a general consequence of the comparison procedure itself, but was specifically amplified by conditions involving temporal cueing, action generation, or additional sensory stimulation.

Regarding our results, the observed regression might reflect a specific degree of uncertainty associated with presented visual cues or self-generated actions, leading to a stronger adaptation toward the mean. A higher degree of uncertainty and the resulting steeper regression could, according to inference and predictive coding frameworks, reflect a stronger reliance on prior expectations (Ma & Jazayeri, 2014). In contrast to classical forward model accounts, Bayesian predictive frameworks do not conceptualize sensory attenuation as the active cancellation of self-generated sensory input. Instead, they assume that the brain continuously attempts to infer and explain (the causes of) sensory events by integrating prior expectations with incoming sensory evidence (Clark, 2013; Friston, 2005, 2010; Rao & Ballard, 1999). A small prediction error thus reflects the small amount of new information within a predicted stimulus. Since we

conducted a behavioral design, no conclusions regarding the neural responses can be drawn. Importantly, predictive processing accounts do not necessarily predict perceptual attenuation as consequence of successful prediction. Depending on the precision weighting of sensory evidence and prior expectations, predictable stimuli may under some circumstances even be perceptually enhanced rather than attenuated (Press et al., 2020; Yon et al., 2021). Study 1 and Study 2 showed that no experimental circumstances differed except for the presented volume, indicating that the observed regression-to-the-mean effects might reflect an inferential process regarding stimulus intensity that is stronger in uncertain situations.

Crucially, these findings of a regression itself indicate that perceived intensity depends primarily on the sensory context rather than on whether a stimulus is self-generated. The dependence on specific loudness contexts is consistent with predictive coding accounts, according to which prior expectations and current sensory input are continuously integrated in order to minimize prediction errors (Rao & Ballard, 1999). In Study 1, two groups of participants were adapted to either a high- or low-intensity context. During the test phase, 80 % of trials corresponded to the adapted intensity level, while 20 % deviated from it. When the majority of stimuli were drawn from a high-intensity distribution, perceived loudness shifted accordingly; the same held for low-intensity contexts. Thus, perceptual judgments were anchored to the mean sound level of the environment, independent of action-related factors. Participants exposed predominantly to high intensities showed stronger perceptual enhancement of lower-intensity stimuli, whereas participants exposed predominantly to low intensities exhibited stronger attenuation of higher-intensity stimuli. Manipulating the contextual intensity distribution leads to a shift of the underlying reference mean, thereby modulating the magnitude of both enhancement and attenuation.

Importantly, an adaptation to the mean sound level following the regression pattern was also observed in Study 2 under temporally unpredictable conditions. In the vibro-tactile group, probe tones occurred unpredictably with the same random delay as in the baseline group. However, due to the simultaneous presentation of a vibration, regression effects were as pronounced as in the self-generated and externally predictable group. These findings suggest that attenuation and enhancement are not distinct phenomena requiring separate explanatory mechanisms, but rather reflect a common adaptive process. Specifically, both effects can be understood as expressions of context-dependent recalibration of perceptual bias. Whenever stimuli become predictable either through self-generation or external cues, leading to a diverted attention away from the sensory event, regression effects become more pronounced. In general, enhancement effects in Study 1 and Study 2 were more pronounced than attenuation effects, despite previous findings suggesting faster neural adaptation to increases than to decreases in sound level (Dean et al., 2008).

In sum, the presence of regression effects can be interpreted as a consequence of uncertainty in perceptual estimates, which may arise from concurrent actions, predictive cues, or additional sensory events (Jazayeri & Shadlen, 2010; Murai & Yotsumoto, 2018; Petzschner et al., 2015) and is congruent with a stronger reliance on priors (Friston, 2010). Sensory attenuation and enhancement appear depending on the stimulus intensity in the auditory domain and are expressions of the described regression toward the mean sound level.

3.2 Active versus passive movement

A central assumption in many accounts of sensory attenuation is that voluntary actions and specifically motor-based predictive signals such as an efference copy play a necessary role in shaping perceptual biases. The classic forward model is grounded in actively generated movements that produce sensory outcomes, which are assumed to be predictable precisely because they are self-generated (Kilteni et al., 2020). Within this framework, no form of externally generated stimulation should lead to comparable attenuation effects, as the system lacks access to an internal motor signal indicating self-causation. The present findings are not entirely consistent with this account. Previous work has already suggested that factors beyond self-generation must contribute to sensory attenuation. For instance, Dogge, Hofman, et al. (2019) demonstrated that prediction can be dissociated from agency, indicating that self-generation is not a necessary condition. Similarly, Han et al. (2021; 2022) reported attenuation effects even under passive conditions, further challenging a purely motor-based account.

As already described before, other studies have reported enhancement rather than attenuation of predicted or self-generated stimuli. For example, Yon et al. (2021) and Thomas et al. (2022) and demonstrated that predicted or expected sensory outcomes can be perceived as more intense, suggesting that prediction does not uniformly lead to attenuation. In Study 1, tones were either self-generated via a key press or externally generated by the computer, but in all conditions their onset was preceded by an additional stimulus such as an predictive cue, such as a flashing fixation cross or moving bars. Critically, the presence and magnitude of the observed regression effects, expressed by attenuation or enhancement, did not differ between self-generated and externally generated conditions. Together, these results question the necessity of efference copy-based mechanisms and suggest that behavioral sensory attenuation might arise from more general predictive or contextual processes. Such a general predictive mechanism is taken into account in hybrid models of sensory attenuation, according to which attenuation effects may arise not only from self-generated actions but also from the interaction of multiple mechanisms contributing to the prediction of sensory input based on cognitive sources (Dogge, Custers, et al., 2019). Parts of the hybrid model may explain the reported volume effects, particularly because they were observed in both self-generated and cued conditions as well as the effect of proprioceptive predictability of self-touch. However, the hybrid model primarily relies on prediction, which appears difficult to reconcile with the findings of Study 2, in which the regression pattern was found to be independent of predictability.

In Study 2, two groups were instructed to actively trigger the tone through their own movements, whereas two other groups received externally generated tones. Notably, regression patterns were not only observed in the active conditions but also in conditions in which stimulus presentation occurred automatically and unpredictably, yet was accompanied by an additional tactile stimulus. Crucially, self-generated movements did not result in significantly stronger regression effects compared to unpredictable conditions without movement. However, the group that performed active movements and simultaneously received tactile feedback showed descriptively the strongest effects.

In the tactile domain, the reported findings are more consistent with the view that attenuation reflects an updating of proprioceptive estimates of limb position within the body schema, rather than a mere consequence of motor-based prediction. From this perspective, self-touch is not attenuated because it is predicted via a forward model, but because it provides a reference signal for recalibrating internal representations of the body and the spatial relations between limbs. One

expects an evoked response of somatosensory after experiencing repeated self-touch, which builds up prediction. Critically, this process does not depend on the presence of voluntary motor commands. By experimentally decoupling efferent signals from their sensory consequences through passive limb transport, it was possible to demonstrate that attenuation persists even in the absence of action. This finding aligns with previous work showing that tactile attenuation can occur independently of active movement (Dogge, Custers, et al., 2019; Kilteni et al., 2019).

What appears to be essential, therefore, is not the execution of an action per se, but the availability of a reliable proprioceptive prediction about the sensory consequences of limb position, in this case self-touch. This interpretation is difficult to reconcile with active inference accounts, which propose that sensory attenuation reflects a temporary reduction in the precision weighting of sensory evidence during active movement execution in order to allow proprioceptive predictions to guide action (Brown et al., 2013). Moreover, the observation that attenuation was present even in atypical limb configurations, such as reversed positions, suggests that the underlying mechanisms operate on flexible, continuously updated internal body representations rather than on fixed motor predictions (Ehrsson, 2007; Lenggenhager et al., 2007). After systematically isolating different sources of predictability including temporal, visual, and spatial cues, proprioceptive predictability remained the only factor sufficient to elicit attenuation of self-touch.

Taken together, the findings from both the auditory and tactile domains challenge the view that sensory attenuation is primarily driven by forward models and voluntary actions. Instead, they support a more general account in which tactile attenuation arises from proprioceptive recalibration processes that are independent of voluntary movement, while auditory as well as tactile attenuation can emerge from both active movements and externally provided predictive cues.

Across experiments, attenuation was observed even in the absence of voluntary movement, provided that sensory consequences were less attended or predictable either based on proprioceptive information in the tactile domain or temporal cues and actions in the auditory domain. As already stated, this indicates that active movement per se is not a prerequisite for attenuation. Importantly, in Study 2, attenuation-related regression effects were even observed under temporally unpredictable conditions, in which no predictive cues were available and only a concurrent tactile stimulus was present at tone onset. This finding suggests that, at least in the auditory domain, neither self-generation nor prediction is strictly necessary. Instead, predictive cues may primarily act by diverting attention away from the sensory event, thereby increasing perceptual uncertainty and giving rise to the same regression-to-the-mean pattern.

3.3 Temporal predictability and temporal control

The role of temporal predictability has been widely described as crucial for sensory attenuation effects. This applies to passive paradigms (e.g., Dogge, Custers, et al., 2019; Han et al., 2021; Han et al., 2022), as well as to active ones, in which introducing a delay between an action and its sensory consequence has been shown to reduce attenuation (e.g., Bays et al., 2006; Bays et al., 2005; Kilteni et al., 2019).

Across all three studies, a baseline condition with low temporal predictability was included. In Study 1, the same stimulus intensities were presented as in the self-generated and externally predictable conditions, but stimulus onset followed a random delay of 500 to 3000 ms after trial start. This manipulation reduced temporal predictability of stimulus occurrence. The same approach was applied in Study 3, where touch onset in the baseline condition was likewise randomized within a 500 to 3000 ms interval. In Study 2, the same baseline condition as in Study 1 was used as a control condition without temporal prediction or cues.

Importantly, sensory attenuation, or more precisely, regression-to-the-mean patterns, were observed not only in active but also in passive conditions, as described above. This finding argues against a necessary role of temporal control, as temporal control was only present in the active conditions. Specifically, the flashed and continuously cued conditions in Study 1, the external, blind, speed-controlled, spatio-temporally cued, and recalibrated conditions in Study 3, and the vibration condition in Study 2 did not involve temporal control, yet still exhibited the same effects as conditions involving self-generation. However, the specific contribution of temporal control in self-generated conditions was not systematically disentangled from temporal predictability, as both were inherently linked in the active conditions.

Regarding predictability, another question arises in this context. In auditory paradigms, the association between pressing a button and hearing a tone is comparatively artificial, particularly when contrasted with natural forms of self-touch in the tactile domain. This raises the question of what exactly is predicted during action: merely the timing of any upcoming sensory event, or also the specific identity of the expected sensory consequence. Fuehrer et al. (2022) demonstrated that attenuation-related effects may depend less on movement per se than on the extent to which a specific sensory outcome is anticipated. However, evidence for such identity-specific predictions remains mixed: Dogge, Hofman, et al. (2019) found no convincing evidence for identity-specific motor predictions in sensory attenuation when tones were either congruent or incongruent with previously learned pitch associations. Similar conclusions were reported by Kiepe et al. (2024; but see Bäß et al., 2008; Hughes et al., 2013 for ambiguous results).

These findings are difficult to reconcile with classical ideomotor theory. According to ideomotor accounts, actions are represented in terms of their anticipated sensory consequences, such that executing an action preactivates the expected sensory outcome (Greenwald, 1970; Hommel et al., 2001). Sensory attenuation is therefore interpreted as a consequence of this preactivation: because the sensory effect is already anticipated, the actual sensory input evokes a reduced response (Roussel et al., 2013). Critically, this framework assumes that stable and learned action–effect associations are central for generating sensory predictions (Pfister et al., 2014). However, the regression-to-the-mean patterns observed in Studies 1 and 2 are difficult to explain within such a framework, as they included not only attenuation of loud tones but also enhancement of quiet tones.

At the same time, reduced neural responses do not necessarily translate directly into perceptual attenuation (Press et al., 2020). In this sense, the general notion that sensory predictions are shaped by learned associations may still be compatible with the reported findings. Importantly, the present data in the tactile domain suggest that proprioceptive cues generated during movement were sufficient for establishing action-effect associations based on active or passive movements, whereas purely spatio-temporal cues without accompanying movement appeared insufficient to produce comparable attenuation effects.

In Study 2, the role of temporal predictability was examined in comparison to attentional influences. In Study 1, all experimental conditions were temporally predictable, whereas only the baseline lacked predictability. In that baseline condition, no additional cues were provided, and the two tones were presented after a random delay. In contrast, Study 2 included two self-generated conditions, which were fully temporally predictable and controllable, and two externally generated conditions with random delays prior to tone onset. One of these served as the baseline, while the other included a vibration presented simultaneously with the first tone. While the self-generated conditions showed the expected regression pattern, it is noteworthy that the same pattern was also observed in the vibro-tactile group. The only difference between the baseline and the vibration group was the presence of the concurrent tactile stimulus, as both involved temporally unpredictable tone presentation. Nevertheless, the vibration group produced regression effects comparable to those observed in the self-generated groups.

This finding indicates that neither self-generation nor temporal predictability alone is sufficient to account for sensory attenuation or regression effects. Instead, both may share a common functional role in modulating perceptual processing, potentially by diverting attention or increasing perceptual uncertainty, which in turn gives rise to a regression-to-the-mean bias.

3.4 Role of attention

Building on the regression patterns described above, the last step was to address the underlying mechanisms of the perceptual biases: why does adaptation to the mean occur in both active and passive but temporally predictable conditions, and why does perception systematically regress toward the mean, indicating reduced precision? While Study 1 initially pointed toward a general role of prediction, later findings of Study 2 suggest that the use of predictive cues may represent only one of several factors that introduce distraction, which in turn gives rise to regression effects. Notably, regression patterns were observed irrespective of whether stimuli were predictable or not. Neither voluntary action nor predictability alone systematically modulated the effect. Instead, the mere presence of concurrent sensory or motor demands was sufficient to induce systematic shifts in perceived intensity relative to a neutral baseline condition without distraction. Since these shifts reflected a classical regression-to-the-mean pattern, this pattern can be interpreted as index of uncertainty (Jazayeri & Shadlen, 2010; Murai & Yotsumoto, 2018; Zimmermann & Cicchini, 2020). The presentation of visual cues, additional stimuli, or self-generated actions led to a stronger adaptation toward the mean compared to a neutral baseline.

The observed regression pattern is consistent with findings by Saupe et al. (2013), who proposed that self-generated actions draw attentional resources away from the primary task. Consequently, stimuli receiving greater attentional allocation should be processed more precisely and therefore exhibit reduced attenuation (Jones et al., 2013). Although these findings were originally discussed in the context of attenuation-only effects, the same mechanism could also account for the regression effects observed in Study 1 and Study 2, since attenuation itself appears to represent one expression of the regression. Supporting this interpretation, directing attention toward the target stimulus has been shown to enhance perceptual awareness, which in turn reduces sensory attenuation (Coull et al., 2000; Coull & Nobre, 2008). At the same time, the reported findings stand in contrast to studies stating that sensory attenuation is unaffected by attention (Timm et al., 2013). They also are not in line with accounts proposing that self-generated stimuli are attenuated because they are less surprising, attract less attention, and are consequently processed as more certain (SanMiguel et al., 2013). In this context, Harrison et al.

(2021) argued that sensory attenuation reflects an interaction between prediction and attention. However, the results of Study 2 indicate that prediction was not necessary or sufficient to induce the regression bias. Instead, the diversion of attention appeared to be the critical factor underlying the observed effects.

Regarding predictive processing frameworks, attention has been proposed as a factor that may explain differences between enhancement and attenuation effects. In the present setup, however, attention was allocated equally across all tested volumes, while the observed regression pattern still varied as a function of stimulus intensity. According to Kiepe et al. (2021, 2024), quiet tones may be perceptually enhanced because they require increased attentional resources. This explanation was originally proposed for tones presented near the hearing threshold (Reznik et al., 2015), whereas the present studies used sound intensities of at least 40 dB. Moreover, if attentional allocation alone accounted for the observed effects, enhancement should either have been present in all conditions involving relatively quiet tones, which was not the case in the baseline condition, or in all temporally cued conditions that enabled participants to direct attention towards the upcoming stimulus. The observed pattern suggests a different interpretation. Cueing and self-generation did not appear to focus attention on the expected stimulus itself, but may instead have diverted attentional resources away from the auditory judgment task, thereby increasing uncertainty regarding the perceived sensory input and consequently strengthening regression-to-the-mean effects. This interpretation is further supported by the temporally unpredictable vibration condition in Study 2, in which both the probe tone and the vibration occurred randomly. In this condition, participants could not proactively direct attention towards the upcoming stimulus, yet the regression pattern was still observed.

This interpretation is further supported by the finding that increasing levels of vibro-tactile stimulation during tone presentation led to stronger regression effects. In other words, as the degree of distraction increased, perceptual judgments became less precise and more strongly biased toward the mean. Together, these results suggest that sensory attenuation and enhancement are not only driven by predictive mechanisms, but instead arise from reduced perceptual precision under conditions of distraction. Under uncertain conditions, caused by actions or additional stimuli, observers appear to rely more heavily on priors or the average sensory context, leading to the characteristic regression-to-the-mean pattern (cf. Jazayeri & Shadlen, 2010; Murai & Yotsumoto, 2018; Petzschner et al., 2015; Zimmermann & Cicchini, 2020). Using actions to trigger or cues to announce stimulus onset yields comparable attentional resources than the presented vibro-tactile stimulus in Study 2.

3.5 Limitations and future directions

The presented studies provide interesting insights into the mechanisms and characteristics of sensory attenuation and enhancement. However, several limitations should be considered, which also point to promising directions for future research.

First, two of the three studies focused on the auditory domain, whereas only one addressed the tactile domain. In the auditory experiments, the primary focus was on regression to the mean effects and context-dependent adaptation, reflected in both perceptual enhancement and attenuation. In contrast, the tactile study concentrated on self-touch recalibration and different aspects of prediction. Although both domains consistently showed that attenuation can occur in the absence of self-generated action, the findings should not be directly generalized across

modalities (cf. Giannini et al., 2025). For instance, investigating regression effects in the tactile domain would require systematically varying stimulation intensities across a range centered around a meaningful perceptual mean, comparable to the auditory paradigm. If similar Bayesian or central tendency mechanisms operate across sensory modalities, one would expect a comparable pattern in the tactile domain, namely enhancement of weaker stimulation and attenuation of stronger stimulation. Next to the auditory domain, such modality-general central tendency effects have also previously been reported across visual perception and have been linked to sensory uncertainty and prior integration (e.g., Murai & Yotsumoto, 2018).

To further examine the role of attentional diversion in the tactile domain, future studies could introduce concurrent stimuli either within the same modality or across modalities. However, in the present experiments of Study 3, the inclusion or exclusion of visual and auditory cues before stimulus presentation did not systematically alter attenuation effects. Moreover, active movement itself cannot be unambiguously interpreted as a distractor, as it was present in conditions both with and without attenuation effects. If attentional factors do contribute in the tactile domain, they might be closely linked to proprioceptive prediction, which was identified as a key factor in tactile attenuation during self-touch. Nevertheless, the current data do not provide direct evidence for a primary role of attention in this domain (but see Cao & Gross, 2015).

Importantly, although the present findings do not provide support for forward model accounts in their classical form, they cannot conclusively rule out the possibility that forward model-related mechanisms contribute to sensory attenuation under certain conditions. At the same time, the observation of behavioral attenuation or regression effects in passive conditions suggests that classical efference copy-based accounts would require theoretical refinement, as motor-command-based predictions alone do not appear sufficient to explain the present findings. It remains conceivable that active and passive movements as well as diverted attention rely on partly distinct mechanisms that produce similar perceptual outcomes, for example through proprioceptive, temporal, or contextual predictions that can arise even in the absence of voluntary action.

At the same time, self-touch represents a highly specific case, typically involving two body parts with the acting and the receiving limb. This configuration has no direct analogue in the auditory domain and is therefore difficult to translate across modalities, particularly with respect to the role of proprioceptive predictability. Consequently, attenuation effects observed in one sensory domain cannot be assumed to generalize to others without qualification. Future research should therefore aim to better characterize both domain-specific mechanisms and potential cross-modal principles, in order to identify which aspects of sensory attenuation reflect general perceptual processes and which are modality-specific (cf. Giannini et al., 2025).

Interestingly, no significant or particularly pronounced effects were observed in the JNDs. This is especially surprising in the auditory experiments, in which regression to the mean effects were clearly present, yet were not reflected in the JND measures. Given that regression is commonly interpreted as a consequence of increased uncertainty, one might expect corresponding changes in JNDs, which are typically used as an index of perceptual uncertainty. However, it is conceivable that the regression pattern itself already captures the influence of uncertainty, thereby reducing or masking any additional effects that might otherwise be observable in JND or other sensitivity measures. In addition, Weiss et al. (2011a) stated that attenuation affects rather a shift in perceptual bias than a change of sensitivity, which would be in line with our results of Study 1-3.

Importantly, all studies reported here rely exclusively on behavioral data. Consequently, no direct conclusions can be drawn regarding neurophysiological markers such as the N1 or P2 components, which are often interpreted as indices of sensory attenuation. In the present work, only participants' responses were analyzed, either to construct psychometric functions or within an adaptive procedure. It therefore remains possible that neurophysiological measures would reveal patterns that differ from the behavioral regression effects observed here. Future studies could combine behavioral and electrophysiological approaches within a unified experimental design in order to directly compare these measures (e.g., Giannini et al., 2025). At the same time, methodological challenges need to be considered. In auditory EEG paradigms, for instance, it may be difficult to obtain sufficiently robust neural responses for low-intensity tones, which could limit the detectability of corresponding ERP components. In the current behavioral paradigm, it remains unclear whether the observed regression effects arise at a perceptual stage or emerge at later decisional stages, such as during comparative judgments or rating procedures. Combining EEG with the present approach could help to disentangle these possibilities by determining whether regression-related modulations occur immediately following stimulus presentation or only at later stages associated with decision (Harrison et al., 2021).

In Study 3, one finding merits closer consideration: the descriptive statistics indicate a slight enhancement in the baseline condition relative to the physically presented stimulus intensities. One could therefore argue that the observed attenuation effects in the experimental conditions are partly driven by this baseline shift, which increases the difference between baseline and experimental conditions and may contribute to statistical significance. However, it is important to consider that in paradigms involving two consecutive tactile stimuli, the perception of the second stimulus may be reduced because the somatosensory system has not fully recovered from the initial stimulation (Gescheider et al., 1979; Verrillo et al., 1983). At the same time, this limitation applies equally to all conditions, as the inter-stimulus interval was held constant throughout the experiment. Notably, despite this general bias favoring the first stimulus, the experimental conditions predominantly showed attenuation effects, which even strengthens the interpretation of these findings. The inclusion of a baseline condition therefore appears essential, as it highlights the influence of methodological factors on perceptual judgments. Future studies could address this limitation by employing non-comparative paradigms, such as numerical rating or magnitude estimation tasks, which reduce dependencies between sequential stimuli (Petzschner et al., 2015).

A further point that highlights a deeper issue in sensory attenuation research is the lack of standardized methods and terminology. As a result, some studies report attenuation only for self-generated stimuli but not for externally generated ones, whereas others consistently find enhancement effects while ostensibly investigating the same phenomenon. In the auditory domain, Study 1 attempted to suggest a coherent account in terms of regression to the mean; however, in the tactile domain, a unifying explanation is still lacking. For example, Kilteni et al. (2020) employed a paradigm similar to that used in Study 3 and did not observe attenuation under passive conditions. Notably, their study used comparable probe intensities (approximately 2 N) and similar measurement approaches (psychometric functions), yet yielded different results. This suggests that additional variables, such as participant training, task demands, task instructions, or the ecological validity of the setup may critically influence outcomes. The presence of these uncontrolled factors makes it difficult to directly compare findings across studies and contributes to challenges in reproducibility (cf. Dogge, Custers, et al., 2019).

In addition, both auditory studies primarily employed a blocked design for volume presentation, which likely facilitated predictions about the upcoming stimulus, as the volume remained constant within each block. Despite this high level of predictability, the regression effect was still observed, which again underlines the cruciality of diverted attention. It would therefore be informative to examine whether the regression becomes more pronounced when volumes are randomized on a trial-by-trial basis, thereby increasing uncertainty.

Ecological validity represents an additional important consideration, as sensory attenuation paradigms risk being reduced to artificial laboratory phenomena. While Study 3 aimed to approximate self-touch under controlled conditions, the touches were still applied by a wooden rod after participants had been moved on a custom-built carrier. Additionally, several aspects of the auditory paradigms in Study 1, such as the use of a flashing fixation cue or two moving bars to induce temporal predictability, are not representative of real-world sensory experiences. Although such cues are methodologically useful for isolating specific mechanisms, they may limit the generalizability of the findings. Previous work has emphasized that predictive processes in natural environments are typically embedded in richer, multisensory, and context-dependent settings rather than being driven by isolated cues (de Lange et al., 2018; Press & Yon, 2019). Future research should therefore aim to investigate sensory attenuation in more ecologically valid paradigms that capture the complexity of real-world perception, for example by incorporating naturalistic actions, continuous sensory streams, or virtual reality environments.

4 Conclusion

The aim of this dissertation was to investigate the origins and mechanisms underlying sensory attenuation across the auditory and tactile domains. In the auditory domain, attenuation effects were found to reflect a regression-to-the-mean pattern. Specifically, lower-intensity tones were perceptually enhanced, whereas higher-intensity tones were attenuated. The transition point was observed around 60–70 dB, corresponding to typical environmental sound levels. Importantly, this pattern was shown to depend on the sensory context to which participants were exposed. As demonstrated in Study 1, these effects occurred in both active and passive conditions, thereby challenging the forward model as a sole explanation and instead pointing toward a more general mechanism related to contextual adaptation and prediction. Study 2 further addressed why predictive conditions give rise to regression effects. Contrary to initial expectations, increased predictability was associated with reduced perceptual precision. The findings suggest that prediction itself is not the only driver of the effect. Rather, predictive cues and self-generated actions appear to divert attentional resources away from the perceptual task, leading to increased uncertainty and, consequently, regression toward the mean. Consistent with this account, the magnitude of regression scaled with the degree of distraction: stronger concurrent vibrotactile stimulation during tone presentation resulted in steeper regression effects.

In the tactile domain, attenuation was again observed for both active and passive movements leading to self-touch. Systematic manipulations of different forms of predictability indicated that temporal, visual, or external cues were not necessary to elicit the effect. Instead, proprioceptive predictability emerged as the critical factor underlying tactile attenuation. Furthermore, this proprioceptive prediction was shown to be flexible and amenable to recalibration. Attenuation persisted even when limb configurations were altered, provided that the resulting position could be reliably inferred from prior movement and current arm position.

Taken together, the findings of this dissertation suggest that motor-based forward models alone may not fully account for sensory attenuation effects. Instead, they might support a more comprehensive account in which attenuation and enhancement arise from context-dependent adaptation and reduced perceptual precision under conditions of distraction in the auditory domain, and from proprioceptive recalibration processes in the tactile domain.

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6 Affidavit

Eidesstattliche Erklärung gemäß § 5 der Promotionsordnung vom 15.06.2018 der Mathematisch-Naturwissenschaftlichen Fakultät der Heinrich- Heine-Universität Düsseldorf:

Ich versichere an Eides Statt, dass die Dissertation von mir selbständig und ohne unzulässige fremde Hilfe unter Beachtung der „Grundsätze zur Sicherung guter wissenschaftlicher Praxis an der Heinrich-Heine-Universität Düsseldorf“ erstellt worden ist. Die Dissertation wurde in der vorliegenden oder ähnlichen Form noch bei keiner anderen Institution eingereicht. Ich habe bisher keine erfolglosen Promotionsversuche unternommen.

Düsseldorf, Mai 2026 _____

Saskia Johnen

7 Acknowledgements

First of all, I would like to thank my supervisor, Prof. Dr. Eckart Zimmermann, for giving me the opportunity not only to pursue a PhD, but also to learn, grow, and experience so much over the past three years. I have had the chance to experience and achieve many things, and most of this would not have happened without your support in the first place. Your motivation and passion for science are truly unmatched and inspiring; you always bring new ideas and creative ways of thinking to the lab. Me, my research and I have benefited a lot from our extensive meetings and our constant exchange. I would also like to extend my appreciation to Prof. Dr. Christian Bellebaum; thank you for promptly taking on the role of secondary supervisor.

Throughout my PhD, I had the honor of working with many special people who supported and guided me along the way. I would like to begin with Clara, Manu, and Sandy — you made my start as smooth as possible and taught me everything I needed to know, from downloading MATLAB, to programming my first experiment, to fitting my first psychometric function. Antonella and Piero, I had the pleasure of having you accompany me throughout my entire PhD, and you were always incredibly supportive. Antonella, you built me up countless times and somehow always found solutions to seemingly unsolvable problems. Umberto, Hanna, and Leonie — my former and current office partners — thank you for watching me change figures from dark pink to light pink and back again thousands of times. Additional thanks for sharing the office and kitchen with me; I could not have imagined a better “girls’ office.” Another special thank you goes to the student assistants who sacrificed themselves to pilot and collect most of the data presented here — Theresa, Sina, Jule, Jara, and Lena, your help is deeply appreciated!

I also want to thank the Mensa crew around Larissa, Carolin, Sandra, Isa, Pauline, and Fabian. Lunch breaks with you always made me smile and distracted me from work, even if only for a few minutes. I also appreciate that you always had an open ear for me, often followed by helpful advices.

Next, I would like to thank my swimming team for instantly lifting my mood as soon as I entered the pool hall. Whenever I needed to talk, you always had warm and encouraging words for me. Jana, you might not know it, but you helped me tremendously and probably saved me from many mental breakdowns by distracting me with your funny stories about your work or house-building adventures. Another thank you goes to Lena, who has probably heard every work-related story at least five times and never got tired of listening during our running sessions. The same applies to Nina and Stephan as well as to my little big sister Annika, for never stopping teasing me. Thank you!

A very special thank you from the bottom of my heart goes to my parents for their endless support and for always letting me follow my own path, fully trusting that things would work out. You probably did not envision this exact path for me, but you never doubted that I would always find what was best for myself.

Last but not least, to the undoubtedly most important person in my life: Sebastian. We have supported each other since school, and you have stood by my side throughout these past three years. You make me a better person in every possible way. I cannot thank you enough for everything you have done and continue to do. Thank you for bringing me dinner when I was stuck at my laptop for hours and did not even realize it had become night. No matter how stressful your own day was, you always made sure that I was okay and had the right amount of chocolate to feel better. You are simply the best, and I could not wish for a better partner!

8 Appendix

Original article of Study 1

Johnen, S., & Zimmermann, E. (2025). Regression to the mean explains perception of action consequences. *Proceedings of the Royal Society B: Biological Sciences*, *292*(2057). https://doi.org/10.1098/rspb.2025.1715

I was the corresponding and first author of this article. I contributed to the development of the paradigm, created the experimental setup, conducted the data acquisition and analysis, contributed to the interpretation of the results, wrote the initial draft of the manuscript, and cooperated with Prof. Dr. Eckart Zimmermann on the following versions of the manuscript.

Original article of Study 2

Johnen, S. & Zimmermann, E. (2026). Cross-Modal Interference Explains Perceptual Biases for Action Consequences. *Psychological Science - Submitted*.

I was the corresponding and first author of this article. I contributed to the development of the paradigm, created the experimental setup, conducted the data acquisition and analysis, contributed to the interpretation of the results, wrote the initial draft of the manuscript, and cooperated with Prof. Dr. Eckart Zimmermann on the following versions of the manuscript.

Original article of Study 3

Johnen, S., Bayer, M., & Zimmermann, E. (2026). Sensory attenuation reflects proprioceptive recalibration rather than motor forward. *iScience – Under Review*.

I was the first author of this article along with the second author Dr. Manuel Bayer. I contributed to the development of the paradigm together with Dr. Manuel Bayer, created the experimental setup together with him, conducted the data acquisition and analysis, contributed to the interpretation of the results, wrote the initial draft of the manuscript, and cooperated with all co-authors on the following versions of the manuscript.

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Research

Cite this article: Johnen S, Zimmermann E. 2025 Regression to the mean explains perception of action consequences. *Proc. R. Soc. B* **292**: 20251715.
https://doi.org/10.1098/rspb.2025.1715

Received: 2 July 2025
Accepted: 2 September 2025

Subject Category:
Neuroscience and cognition

Subject Areas:
behaviour, cognition, neuroscience

Keywords:
sensory attenuation, sensory enhancement, adaptation to mean sound level

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Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.8026808.

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Regression to the mean explains perception of action consequences

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SJ, 0009-0002-8275-7471

Predictions shape the perceptual consequences of our own actions such that self-generated events appear less intense to us. However, recent studies also reported sensory enhancement of self-produced sounds. Here, we tested whether sensory attenuation and enhancement are signatures of an adaptation to the mean sound statistics. In 330 human participants, we tested the idea that predictions about upcoming sounds shift auditory processing to the average sound context. Participants produced sounds between 40 and 80 decibels (dB) and rated their loudness. Estimates of perceived loudness followed a regression to the mean sound level. The effect was similar for self-produced and passively observed but temporally predictable tones, suggesting predictability alone drives perceptual changes. We then artificially created a new mean sound level by presenting sessions in which subjects mostly (80% of trials) produced either loud (80 dB) or quiet (40 dB) tones. In loud contexts, rarely presented quiet tones were enhanced, and in quiet contexts, loud tones were attenuated. Our results challenge the dominant forward model explanation, which attributes sensory attenuation to predictive suppression of self-generated stimuli, and instead open the door for alternative explanations. Our findings point to regression towards the mean sound level as the most plausible account for predictable sounds.

1. Introduction

How predictions shape perception is one of the major threads underlying current perceptual neuroscience. Several models compete to explain the impact of prediction on experience. The testbed of these theories is all instances in which predictions shape sensory experiences. Predictions can suggest the identity of a stimulus or its appearance in time or space. Internal summaries of natural statistics that describe the prevalence of stimuli in natural environments are the most likely driving predictions of stimulus identity [1–3]. Predictions about the time and space of stimulus appearance can be derived from internal or external cues. Predictability of stimulus occurrence is almost perfect when we produce them with our own actions. An abundance of studies has shown that our brains treat self-produced sensations differently than those externally produced. All-day phenomena like the inability to tickle ourselves or the question of why our own voice sounds different to ourselves testify to the impact of predicting the sensory consequences of our own actions [4–8].

The favourite account of sensory attenuation contains a forward model architecture whose aim it is to reduce the perceived intensity of self-produced stimulation when predicted and actual sensations match [5,9] (figure 1). The forward model is built up by an efference copy to arrive at a prediction about the upcoming sensory stimulation. Three types of findings currently challenge the forward model as an explanation of sensory attenuation.

First, the prediction of stimulus identity might be irrelevant for attenuation to occur. To attenuate only the self-produced stimulation from the sound spectrum, the prediction must entail its unique features, which in the auditory case is loudness or pitch. Unlike in self-touch, where the execution of a motor plan to touch one's own body necessarily leads to a tactile sensation on that part of the body, pressing a button does not regularly result in the presentation of a sound. Without training, a connection between the button press and the sound cannot be established. Dogge *et al.* [10] trained subjects to learn certain key tone associations. However, they found no evidence for identity-specific motor predictions in sensory attenuation, neither on a perceptual nor on a neurophysiological level.

Second, studies have reported not only attenuation of self-produced stimulation but also enhancement. While many studies reported that self-produced sounds appeared quieter [11–15], surprisingly, several recent studies also found the opposite that self-produced sounds were judged as louder [11,12,15–17]. This seeming paradox of contradictory evidence needs to be resolved to understand how self-produced sounds are processed by the brain. A hint in this direction was provided by Reznik *et al.* [12], who found attenuation and enhancement in the same study. They reported that self-produced sounds of 75 dB appeared attenuated, whereas sounds close to the individual acoustic threshold appeared enhanced.

Third, some studies have shown that attenuation occurs not only for actively produced but also for passively observed or externally generated stimuli [18,19]. This suggests that the temporal prediction of an event might be sufficient to induce sensory attenuation. However, the literature remains inconclusive about the necessity of an active self-generation compared with equally predictable stimuli. For example, Lange [20] and Klaffehn *et al.* [21] reported attenuation only for self-generated actions compared with passively generated stimuli, while Han *et al.* [18,19] demonstrated that sensory attenuation can also occur in the absence of movement. Supporting this view, Dogge *et al.* [9] argued that predictive mechanisms underlying attenuation do not necessarily depend on self-generation and may go beyond it. In this paper, we sought to study the differences between self-generated and externally generated but temporally predictable stimuli.

An alternative approach to sensory attenuation and enhancement is Bayesian inference. Whereas the forward model operates with concrete sensory predictions based on self-generated stimuli, Bayesian theories rely more on probabilistic inferences about sensory states. In Bayesian perception, uncertain current input is interpreted relative to prior assumptions. Bayesian models suggest that current sensory evidence is combined with prior knowledge about the stimulation, thus enhancing or attenuating the perceived intensity of predicted stimulation [22,23]. By contrast, the forward model cannot explain sensory enhancement [22,24,25].

In a pilot study, originally designed to investigate differences between self- and externally generated stimuli under conditions of predictability and unpredictability, we unexpectedly found enhancement effects for self-generated sounds as well. Notably, we used a sound level of around 49 dB [26], whereas studies reporting attenuation effects often presented sound levels between 60 and 75 dB [12,20]. The parallel evidence for sensory attenuation and for sensory enhancement might indicate that both have a common, yet overlooked, cause. In the present study, we hypothesized that the concurrent existence of attenuation for loud and enhancement for quiet tones [12] might be the signature of a regression towards an average sound level, consistent with the statistical phenomenon known as regression to the mean, where extreme values tend to move closer to the mean. Regression to the mean effects have been observed, for instance in time reproduction tasks, suggesting that the brain takes into account knowledge about temporal uncertainty to adapt internal timing mechanisms to the temporal statistics of the environment [27,28].

Regression effects in loudness perception might be connected to the dynamic hearing shift that adapts the internal sound range to the current acoustic context. Neural populations coding sound level have been shown to use adaptation in order to retain efficiency in animals [1,29–36] and in humans [37,38]. The challenge in loudness discrimination lies in the huge range over which the brain must remain operative. Humans can discriminate sound levels across a 120 decibel (dB) range although neural population codes in the auditory nerve only have a dynamic range between 30 and 40 dB. To cover the entire 120 dB, the dynamic range must be constantly shifted to the current context, i.e. the current sound level statistics [29,39]. Trying to understand someone whispering will produce a different sound level adaptation than when listening to loud music. Different auditory backgrounds can shape your current perception (figure 1A). Sound level adaptation has been investigated in single-cell recordings, and it was found that neurons adjust their responses to the mean, variance and more complex statistics of sound level distributions [29,30]. The increase in coding accuracy near the most commonly occurring sound level should lead to an attractive bias for sound levels outside the adapted dynamic range. The average sound level in all-day human activities is about 50–60 dB. An attractive bias towards this average would lead behaviourally to an attenuation of louder tones and an enhancement for quieter tones. The time course of adaptation is extremely fast with a time constant across neurons of 160 ms [30]. It has recently been reported that neurons in the central thalamus react to temporally predictable stimuli with a decrement of sensory gain corresponding to mean sound level adaptation [40].

Here, we investigated whether sensory enhancement and attenuation result from an adaptation to the average sound level. In this view, quiet tones should result in an enhanced loudness, while louder tones should lead to attenuation. We assumed that predictability of the sound presentation would shift the neural population into adaptation to the mean sound level, resulting in a sensory central tendency. Based on the findings of Reznik *et al.* [12] and our own pilot study [26], we expected a regression to the mean pattern. Producing a tone actively allows perfect temporal predictability about its occurrence. However, we also tested whether passively observed cues indicating tone appearance would affect regression to the mean sound level equally. If the occurrence of tones is as temporally predictable as that of self-generated ones, we would expect to find a similar regression tendency pattern, suggesting that the presence of an efference copy may not be necessary.

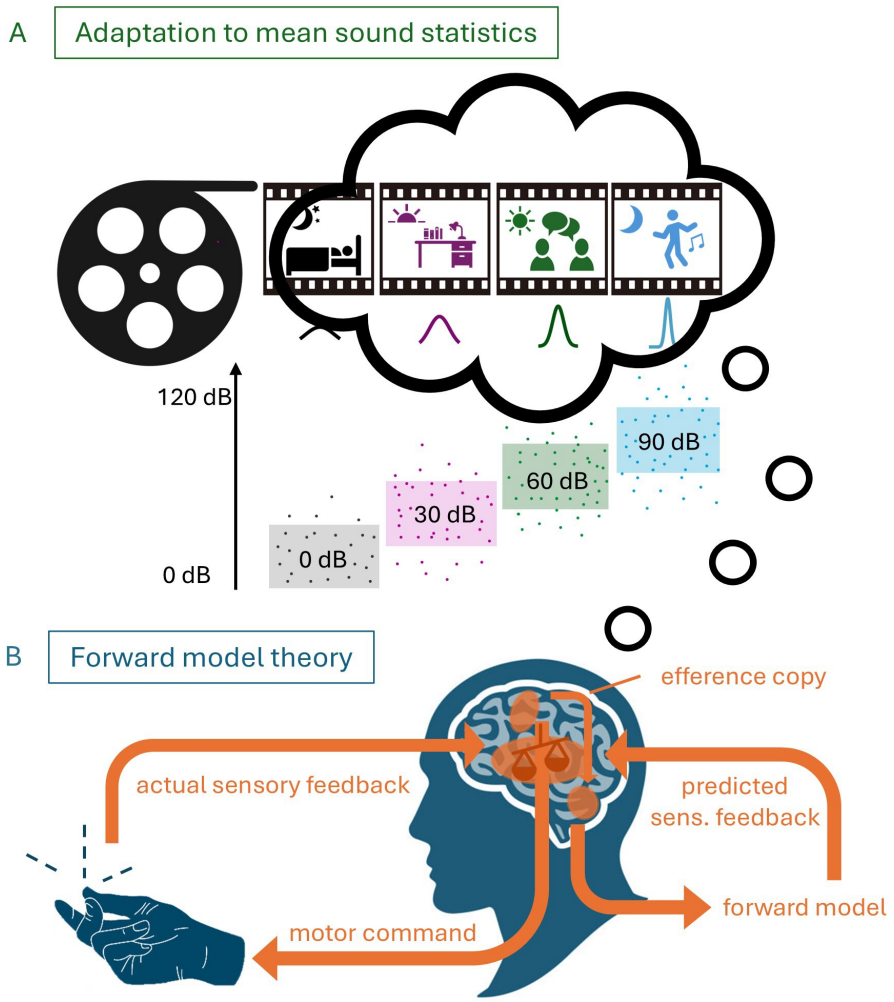

Figure 1. Schematic of adaptation to the mean and the forward model. (A) Different auditory contexts a person has been exposed to over 1 day. According to our theory, this will shape the perception of upcoming stimuli. Coloured boxes show dynamic hearing range that adjusts according to specific contexts. (B) Forward model theory demonstrates the assumed necessity of an efference copy to cause sensory attenuation effects. According to this theory, only self-produced actions can lead to a match between actual and predicted sensory (sens.) feedback.

2. Methods

(a) Materials and procedures for experiment 1

In total, 110 out of 125 tested participants (M_{age} = 22.01 years, s.d. = 3.55 years, 95 female) were analysed in experiment 1. Fifteen participants who provided incorrect responses in more than 25% of the trials with the loudest or quietest reference level were excluded from the analysis. The sample size was chosen to be the same as in a piloting study [26], which was n = 55 per group. Participants were randomly and equiprobably assigned to one of two groups. All of them were seated in front of a Dell P2419H Screen with a refresh rate of 60 Hz, that was placed 57 cm away from them. The experiment was built and run in MATLAB [41] using the Psychophysics Toolbox v.3 [42–44]. Used headphones were JBL Tune 500 or Speedlink Garon that were connected via cable to the computer. Physical sound levels of the headphones were measured by a sound level metre (B&K 2250 by Brüel and Kjær). Every used tone was presented for 300 ms with a frequency of 1 kHz. The keyboard was placed 30 cm away from the table edge. After giving their informed consent, the participants received a pseudomized code and participation number.

In all tested groups and volume conditions, participants were instructed to keep their gaze directed to a white fixation cross (1° × 1°), presented in the screen centre. In the baseline group, participants were asked to rate which of two presented tones appeared louder. After trial start, the first, i.e. the probe tone, appeared after a random interval between 500 and 3000 ms, a procedure similarly employed in a recent study by Fritz *et al.* [45]. The second, i.e. the comparison tone, was presented 500 ms later. Probe tones were presented in one out of five possible sound volumes (40, 50, 60, 70 or 80 dB) per trial. Every probe volume was presented block-wise but in a randomized order for every participant. For each of the five probe volumes, the respective comparison tone was presented in one out of seven possible sound volumes, which were symmetrically centred around the probe sound volume with a step size of 2 dB. In the 40 dB condition, the comparison tone could have 34, 36, 38, 40, 42, 44 or 46 dB. Each comparison tone was repeated 10 times, resulting in a total of 350 trials per session. After the presentation of the comparison tone, participants responded by pressing the left or the right arrow button. In the active group, participants first touched a mark on the table edge before moving to the keyboard to press the space bar and generate the probe tone. The rest of the trial remained identical to the baseline group. Figure 2A,B illustrates one exemplary trial for both groups.

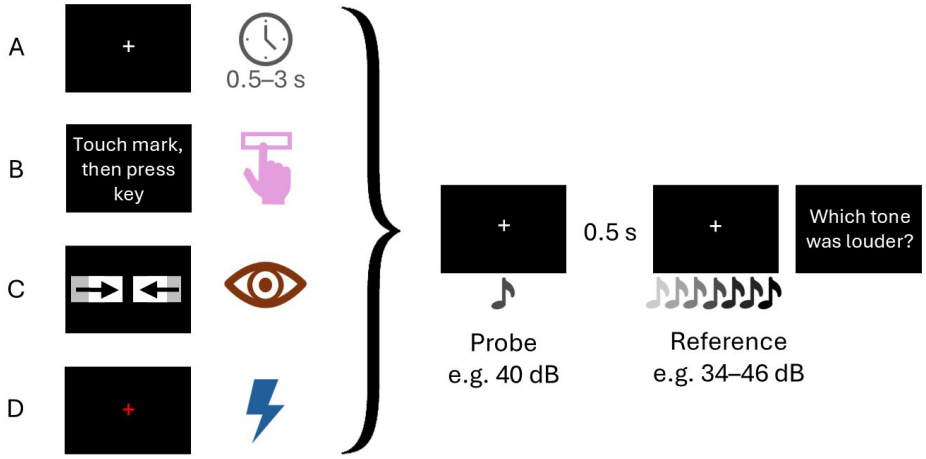

Figure 2. Illustration of experimental trials for experiments 1 and 2. (A) Random interval in the baseline until the appearance of the first tone (experiment 1). (B) Participants triggered the probe tone by pressing a key (experiment 1). (C) The probe tone appeared when two moving bars made contact (experiment 2). (D) A flashing fixation cross served as a cue for the appearance of the probe tone 700 ms later for a duration of 300 ms (experiment 2).

(b) Data analysis

For every probe tone, responses for each comparison were averaged within every participant. To these data, a cumulative Gaussian function was fitted. The mean of the psychometric functions was used as the point of subjective equality (PSE) between the two presented tones and served as an index of perceived loudness. For inferential statistics, we planned to analyse the single-subject PSEs by repeated-measures ANOVAs. Raw data files and all used scripts are available at Open Science Framework [26].

3. Results of experiment 1: dependence of sensory attenuation on stimulus volume

Responses were analysed as psychometric functions to measure the PSE for every participant (figure 3A). A repeated-measures ANOVA revealed a main effect of presented sound level ($F_{4,432} = 24.02$, $p < 0.001$, $\eta^2 = 0.09$) and an interaction of sound level with the between-subject factor group ($F_{4,432} = 4.80$, $p < .001$, $\eta^2 = 0.02$). Figure 3B shows the average perceived loudness as a function of the probe sound level for data measured in the baseline (shown in grey) and in the active group (shown in pink). Baseline data show a systematic negative relationship between loudness estimates and probe level. The quieter the probe tones, the more subjects overestimated them as indicated by the negative slope of the linear fit function. Slopes were used as an index to quantify the strength of the regression. In the active group, we found a negative slope between perceived loudness and probe level that was twice as steep compared to the baseline group. Generally, participants overestimated quiet and underestimated loud tones, a response pattern best described as an adaptation to the average sound level (figure 3C). The average adaptation index of the active group was significantly higher than baseline, $t(108) = -2.30$, $p = 0.024$, $d = -0.44$, s.e. = 0.20.

We then wondered whether the observed regression to the mean reflected the acoustical context that subjects experienced before participating in the experiment or if it was driven by the stimulus distribution itself. To this end, we chose the minimal (40 dB) and the maximal (80 dB) intensities for an exploratory analysis from our probe sound distribution and selected all participants for whom the corresponding blocks of trials were presented either in the first or in the second half of the experiment. When presented in the second half of the experiment, the minimal intensity had been preceded only by louder tones and the maximal intensity only by quieter tones. The selective sampling should have skewed the internal sound distribution, thus amplifying adaptation. Indeed, we found a significant difference for the minimal and maximal probe intensities being presented in the first or second half of the experiment (repeated-measures ANOVA, $F_{1,104} = 6.05$, $p = 0.016$, $\eta^2 = 0.06$, figure 3D). These results indicate that adaptation to the mean sound level updates quickly enough to incorporate the sound statistics of the experimental session.

4. Methods of experiment 2

Next, we investigated why adaptation to the mean sound level increased in the active group in experiment 1. We assumed that actively producing a tone would allow a precise prediction about its temporal occurrence. If temporal prediction led to a shift in the neuron population activity towards the expected volume, then a mere temporal cue should suffice to increase adaptation strength. Here, we aimed to test whether the same regression appears also for passively generated sounds with different levels of predictability. In total, 110 out of 123 tested participants ($M_{age} = 21.35$, s.d. = 2.93, 94 female) were analysed in experiment 2. Thirteen participants who provided incorrect responses in more than 25% of the trials with the loudest or quietest reference level were excluded from the analysis. In the first passive group, a continuous cue was introduced: two white bars (size: 5.3° × 1°) were shown that moved towards each other starting at −6.75° and +6.75° and made contact in the screen centre after 70 frames. Here, the probe tone was presented simultaneously when the bars made contact. In the second passive group

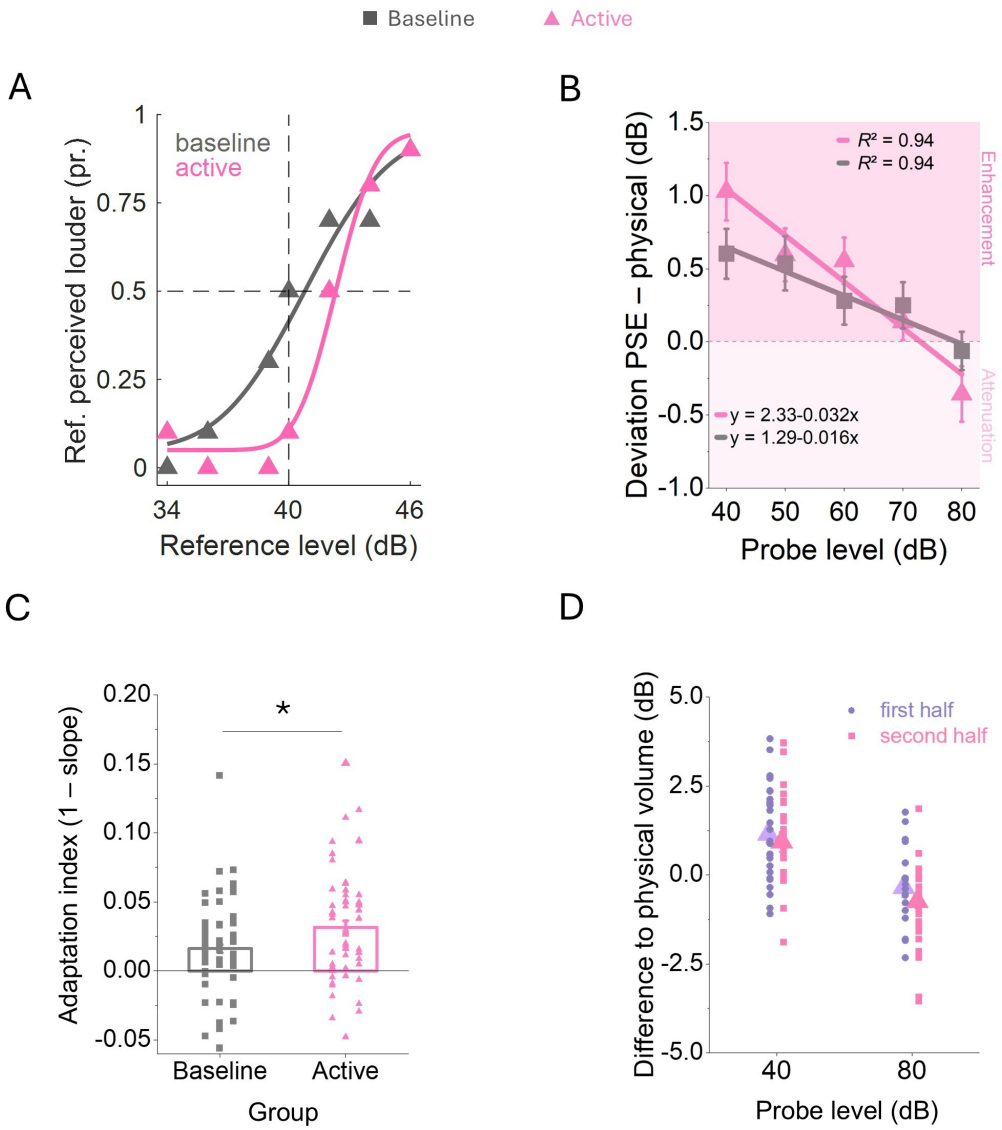

Figure 3. Results for experiment 1: attenuated versus enhanced perception (active). (A) Psychometric functions of one representative participant each. (B) Average loudness estimates shown as the difference to the physical sound level for the baseline (shown in grey) and the active group (shown in pink). Solid lines represent linear functions that best fitted the data. (C) Single subject slopes of the linear fits as the adaptation index for the baseline and the active group. Bars show the mean slopes. (D) Single-subject differences from physical volume for 40 and 80 dB probe levels, separated for the first and second halves of the experiment. Triangles indicate the mean. In all panels, error bars represent s.e.m. *$p < 0.05$

(flashed-cue passive group), 700 ms after trial start the fixation cross flashed red for 300 ms. The colour change served as a cue for the tone, which always appeared 300 ms later. Used materials and programmes remained the same as in experiment 1. Figure 2C,D illustrates one exemplary trial for each group.

5. Results of experiment 2: sensory consequences for passively generated, cued stimuli

A repeated-measures ANOVA based on the PSE differences of the continuous, flashed and baseline groups revealed a main effect of presented sound level ($F_{4,648} = 47.36$, $p < 0.001$, $\eta^2 = 0.10$) and an interaction of sound level with the between-subject factor group ($F_{8,648} = 3.69$, $p < 0.001$, $\eta^2 = 0.02$) (figure 4A,B). The quieter the probe tones, the more subjects overestimated them as indicated by the negative slope of the linear fit function. An ANOVA of the slopes as the adaptation index for the same three groups revealed a significant effect of group ($F_{2,162} = 7.76$, $p < 0.001$, $\eta^2 = 0.09$, figure 4C). A follow-up Bayesian *t*-test comparing the different groups from experiments 1 and 2 provided moderate evidence in favour of the null hypothesis of no differences between the groups over the alternative, with a Bayes factor of $BF_{10} = 0.32$ (error % = 0.02) between the active and the continuous group, as well as between the active and the flashed group ($BF_{10} = 0.23$, error % = 0.03) and between the two passive groups ($BF_{10} = 0.23$, error % = 0.03). The analysis was performed using a Bayesian *t*-test with a two-sided Cauchy prior distribution centred at zero with a scale parameter $r = 0.707$, as implemented as default in JASP v.0.18.1.0 [46]. Descriptive statistics of mean PSE differences for all groups and sound levels can be found in electronic supplementary material, table S1.

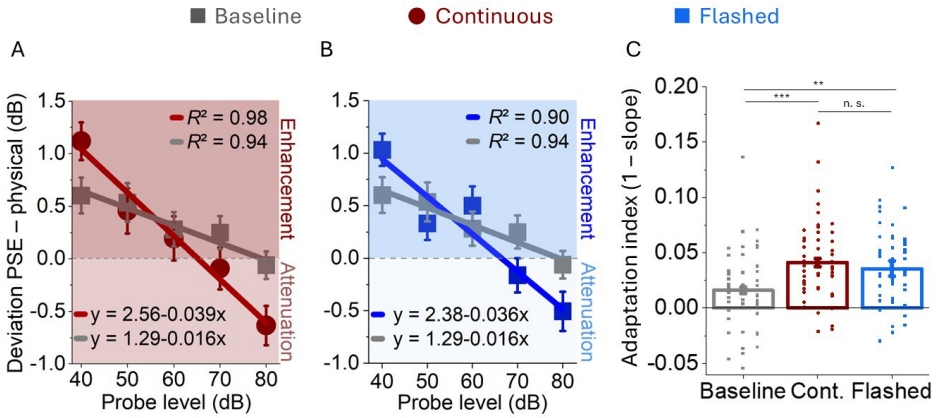

Figure 4. Results for experiment 2: attenuated versus enhanced perception (passive). (A,B) Average loudness estimates shown as the difference to the physical sound level for the continuous (shown in brown), (A), and the flashed-cue group (shown in blue), (B) compared with the baseline (shown in grey). Solid lines represent linear functions that best fitted the data. (C) Single subject slopes of the linear fits as an adaptation index for the baseline, the continuous and the flashed conditions. In all panels, error bars represent s.e.m. $^{**}p < 0.01$, $^{***}p < 0.001$, n. s. not significant.

6. Methods of experiment 3

In experiment 3, we collected data of 118 participants and included 110 in the final sample (M_{age} = 22.16, s.d. = 5.67, 88 female). The desired sample size was chosen to match the size of each group from experiments 1 and 2. Eight participants who provided incorrect responses on more than 25% of the trials with the loudest or quietest reference level were excluded from the analysis. Materials and programmes were identical to experiments 1 and 2.

One group of 56 participants was assigned to a quiet context session, and the other group of 54 participants to a loud context session. The quiet context session started with a baseline condition of 70 trials in which the probe tone was presented with a volume of 80 dB. The comparison tone was presented in one out of seven possible sound volumes (symmetrically centred around the probe sound volume with a step size of 3 dB). The trial structure was identical to that of the baseline group in experiment 1 (figure 2A). Then, a second baseline of 70 trials was measured for a 40 dB probe tone. After the two baseline conditions, another 70 trials were performed in the volume of the desired context (40 dB). During the experimental phase, in the majority of trials (80%, 280 trials), the probe tone was presented with a volume of 40 dB. In the remaining 20% (70 trials), a probe tone with 80 dB was presented. Loud context sessions started with a baseline condition in which a 40 dB probe tone was presented. In the second baseline, an 80 dB probe tone was presented. Since the desired context was 80 dB, participants performed another 70 adaptation trials in that volume. In the loud context condition, in 80% of all trials an 80 dB probe tone and in 20% a 40 dB probe tone were measured. Trial structure during the experimental phase was identical to the one in the active group in experiment 1 (figure 2B), since we only used self-generated trials for experiment 3.

7. Results of experiment 3: adaptation to the mean sound statistics

In experiment 3, we created artificial sound contexts by presenting in 80% of all trials either loud (80 dB) or quiet tones (40 dB). If the context serves as prior and leads to adaptation to the mean sound level, perceived loudness in the test trials should shift towards the context sound level (see figure 5A,B). We expected that when presenting a loud tone to a participant who has been exposed to a quiet context, it should be perceived as more quiet (figure 5A), while the presentation of a quiet tone to a participant who has been exposed to a loud context should lead to an effect of enhancement (figure 5B).

When loud tones were presented in the loud context, they were perceived as intense as in baseline trials (figure 5F). However, the intensity of loud tones intermixed into a quiet context appeared attenuated compared with the baseline (figure 5E). A repeated-measures ANOVA revealed a significant effect of sound level (40 versus 80 dB, $F_{1,108} = 126.21$, $p < 0.001$, $\eta^2 = 0.14$), as well as a significant interaction with the factor context ($F_{1,108} = 17.24$, $p < 0.001$, $\eta^2 = 0.02$), a significant difference to the baseline ($F_{1,108} = 58.93$, $p < 0.001$, $\eta^2 = 0.06$) and again an interaction with context ($F_{1,108} = 12.30$, $p < 0.001$, $\eta^2 = 0.01$).

Figure 5C shows a slight shift in psychometric functions of one representative participant for 80 dB trials that were presented in the quiet context compared with the baseline. Figure 5D shows the corresponding counterpart of 40 dB trials that were presented as rare trials in a loud context, which causes an enhancing shift compared to the baseline. When presented in the quiet context, the loudness of quiet tones was overestimated less (figure 5E). By contrast, when interspersed into the loud context trials, the loudness of quiet tones was massively overestimated by an average 4 dB (figure 5F).Descriptive statistics can be found in electronic supplementary material, table S2.

8. Discussion

Our results show that loudness estimates of self-produced or passively observed but cued tones regress to the average sound level. Observers overestimate the volume of quiet and underestimate the volume of loud tones. In our experiments, regression

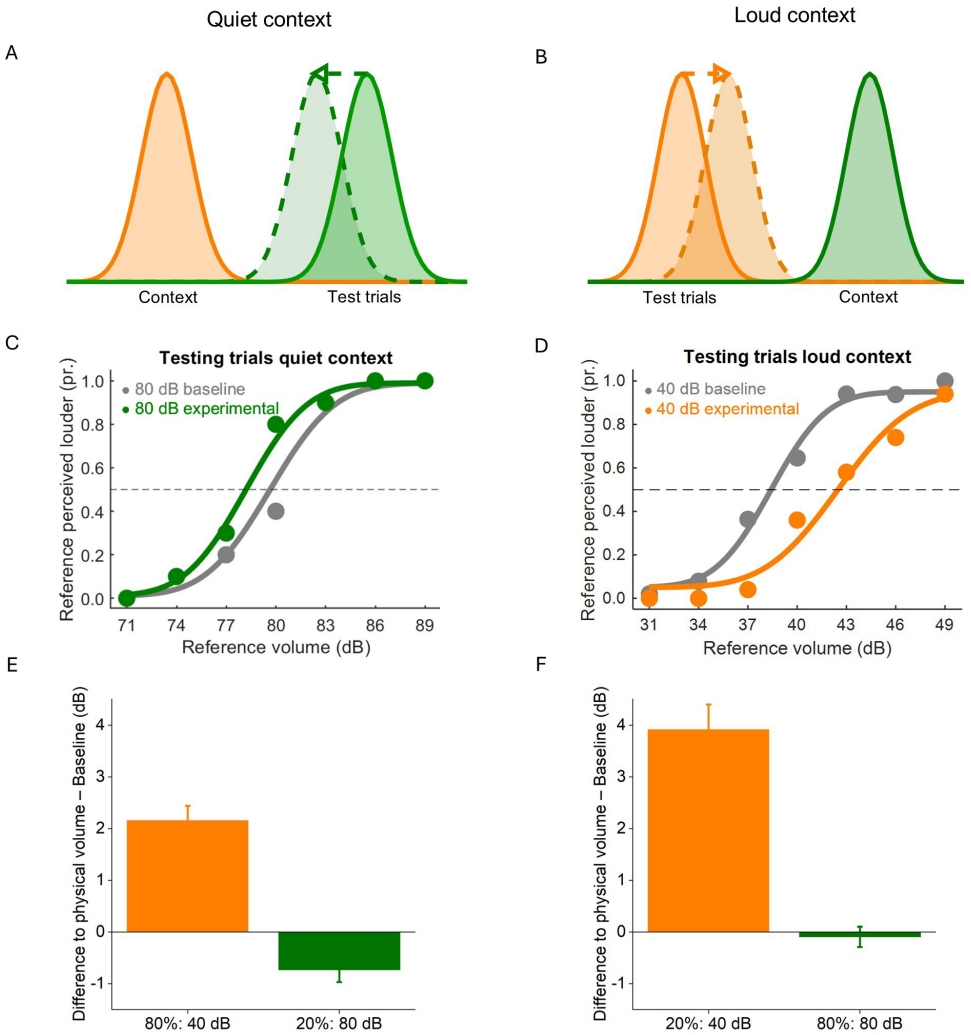

Figure 5. Results for experiment 3: adjustability of the mean sound statistics. (A,B) Schematic of hypotheses. (A) When the context consists of quiet tones (40 dB, shown in orange), loud tones presented in rare test trials (80 dB, shown in green) should shift and appear quieter. (B) When the context consists of loud tones (80 dB, shown in green), quiet tones presented in rare test trials (40 dB, shown in orange) should shift and appear louder. (C,D) Representative psychometric functions of two participants in the quiet and loud context conditions. (E,F) Bar plots showing the mean deviation from physical volume for the majority and minority of presented trials for quiet and loud contexts. In all panels, error bars represent s.e.m.

could already be seen in the baseline, but its magnitude increased in the experimental conditions. We will discuss first the implications of our study for the sensory attenuation/enhancement effects and will then elaborate on the regression to the mean sound level.

Our results have strong implications for the phenomenon called sensory attenuation. They resolve the apparent paradox of concurrent reports showing either attenuation or enhancement in comparable experimental set-ups [11–15,17]. The effects of regression to the mean imply that attenuation and enhancement are two sides of one coin. Both result from a subjective loudness shift to the mean sound level. Attenuation and enhancement are consequences of this shift, emerging when sounds quieter or louder than the average are presented.

In previous research, most studies found sensory attenuation rather than enhancement [47]. Consistent with the regression explanation, the effect was primarily investigated in electroencephalogram studies that used high sound levels (>70 dB) to obtain stronger neural signals. Focusing on the potential functional benefit of sensory attenuation, the forward model provided a mechanistic explanation about the suppression of self-produced sensory stimulation. However, if attenuation and enhancement result from a shift towards the central tendency of sensory stimulation, then the search for dedicated mechanisms to explain these effects should be replaced by a search for what explains the regression.

The forward model account of sensory attenuation has been criticized recently [9,23,48]. Unlike self-produced tactile sensations, it is unclear why sounds should be attenuated in the first place. A piano player's brain would not be well advised to suppress the played sounds. The forward model idea stands on three legs, which are the stimulus identity prediction, the suppression if the prediction is matched by the sensation and finally, the efference copy as an input. Our results indicate that none of the legs of the stool are holding up, as we will now discuss.

First, effects of identity prediction could not be confirmed in a behavioural study [10]. Second, the forward model account is inconsistent with enhancement effects and has been criticized as insufficient [9,23,49]. In our data, sensory enhancement was dominant across a much wider range of probe sound levels than attenuation, which we found only for the loudest sound level. Third, by definition, an efference copy will only be generated in active tasks. In experiment 2, we only used passive cues to mark the appearance of the first tone. We found moderate Bayesian evidence for the hypothesis that the active and passive

groups from experiments 1 and 2 do not differ from each other concerning their strength of regression. The regression to the mean sound level seems to be a general effect that does not depend on the source of generation. Conversely, Arikan *et al.* [50] investigated differences between active and passive movements and their influences on the perception of vibrating stimuli. Even though sensory attenuation was found for both active and passive movements, the active condition still led to larger suppression effects. However, it is not yet clear whether auditory and tactile attenuation effects are comparable or related. In our auditory study, all experimental groups affected the regression equally. This result opens up the possibility that an efference copy is not necessary to produce perceptual changes of self-produced stimuli. The temporal prediction of stimulus occurrence might be sufficient. On the one hand, we cannot exclude the possibility that in active and passive trials separate mechanisms are at play. On the other hand, if temporal prediction produces the regression effects, it is questionable to postulate an additional mechanism that arrives at the similar outcome.

In regression to the mean effects, the perceived intensity of a stimulus results from a weighted average of the actual stimulation and an anchor value [51]. The anchor might consist of a central tendency measure that is derived either from the experimental stimulus distribution or from long-term natural statistics. In real life, the loudness frequency of acoustic stimulation centres around 60 dB, i.e. the human communication sound level. A common research question is which number of samples is necessary to learn or update the sound distribution.

In our experiments 1 and 2, we presented stimuli block-wise with 70 trials per block. Such a presentation order is usually chosen to avoid a regression to the mean stimulus distribution [27]. Yet, we still found regression to the mean effects. It is therefore likely that our data reflect a long-term representation of acoustic statistics that is not yet overwritten by the stimuli presented in the experiment. In experiment 3, we presented an identical sound level, either 40 or 80 dB, over 80% of all trials (i.e. in 350 trials) and found differences when comparing both conditions. Placed within a loud context, quiet tones were judged to be much louder than they actually were. We also found that loud tones presented in a loud sound context were no longer attenuated. These differences suggest that between 70 and 350 trials are necessary to update the internal representation of the sound statistics.

We found a surprisingly strong enhancement effect in the loud context conditions. Given that the increase in enhancement is much stronger than the decrease in attenuation, an additional factor might come into play. Beyvers *et al.* [52] reported more pronounced tactile suppression for strong compared with weak tactile feedback. They suggested that stimuli with weak intensities are upregulated by the perceptual systems to not miss them. In the loud context, quiet tones are presented in only 20% of all trials. It might be that subjects paid additional attention to the tones in the loud context in order not to miss the quiet tones.

Regression to the mean effects might be a signature of an inference about the stimulus intensity. The task of the participants is to judge the intensity of a probe sound that has to be briefly stored in memory to be compared against a reference stimulus. To infer the loudness of the probe sound, the inference process might involve an internal sound representation [53,54]. Consistent with this idea, in experiment 1, regression was already observed in the baseline. This is in line with conclusions from Kiepe *et al.* [53] stating that sensory attenuation is rather based on learnt associations than on generated behaviour [9,55–57]. In a constant process, we use prior information to create predictions about following sensory input. However, regression strength increased when the tone was either self-produced or temporally cued. Temporal predictability of stimulus occurrence might allow a stronger involvement of the internal sound statistic representation to create predictions.

A neural process that supports loudness estimates is the shift of the dynamic sound range. Although we can hear sounds between 0 and 120 dB, precise loudness judgements can only be accomplished with a much smaller range. A dynamic sound range adaptively shifts to the current sound context in order to match this window to the current stimulation. We speculate that the dynamic sound range might shift to the mean of the internal representation. If the mean is located between 60 and 70 dB, our observed regression effects might be the consequence. Adaptation to the mean sound level has been observed in neural responses in the auditory midbrain [1,29,31–35]. Neural adaptation followed an increase in the mean sound level with an average time constant across neurons of 160 ms [30] and might be induced by neurons in the central thalamus that predict temporal stimulus regularities [40]. Since dynamic shifts in auditory neurons are already well documented [30,40], it is likely that this mechanism affects the behavioural perception of predictable tones. Our data show that adaptation to the mean sound level explains why the self-produced sounds appear different to us. Temporal predictions about stimulus occurrence, which are internally available during action planning, might shift the neuron population into adaptation to the mean sound statistics. In humans, Herrmann *et al.* [38] found that neural-response sensitivity is influenced by specific sound-level contexts, and neurons are most sensitive to sound levels that differ from the established and thus predictable context. This might be a neuronal explanation for the strong enhancement effects in the perception of quiet trials in the loud context condition. In our data, the context effect was markedly stronger for the enhancement of quiet tones than for the attenuation of loud tones. Although this link is rather speculative, it was found that neurons adapt faster to increases of loudness than to decreases [30]. If this asymmetry is related to the data of our second experiment, it would explain why quiet tones adapted more strongly to loud tones than *vice versa*.

In conclusion, our data suggest that sensory attenuation and enhancement of self-produced and passively observed, cued sounds stem from a regression to the average sound level. These results challenge the forward model account of sensory attenuation on its main premises.

(a) Limitations

All experiments were conducted in a laboratory setting. In the tactile domain, we can anticipate how self-touch will feel. However, in our experiments, participants pressed a key that triggered a tone. Before the first trials, they had no prior knowledge of how this tone would sound, nor of its volume or frequency. The association between a key press and a tone is rather artificial and may require time to be learnt.

Ethics. Ethical guidelines stated in the Declaration of Helsinki were followed and received approval from the local ethics committee at committee at Heinrich Heine University, Düsseldorf (identification number: 757184).

Data accessibility. Raw data files, all used scripts and supplementary materials are available at Open Science Framework [58].

Supplementary material is available online [59].

Declaration of AI use. During the writing process the authors used ChatGPT in order to improve the flow of certain sentences. After using this tool, the authors reviewed and edited the resulting content as needed and take full responsibility of the publication.

Authors' contributions. S.J.: conceptualization, formal analysis, investigation, methodology, project administration, visualization, writing—original draft, writing—review and editing; E.Z.: conceptualization, methodology, project administration, resources, supervision, writing—original draft, writing—review and editing.

Both authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This project was supported by the European Research Council (project moreSense, grant agreement 757184) and by the Deutsche Forschungsgemeinschaft (DFG, ZI 1456/6).

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Research Article

Main Manuscript for

Cross-Modal Interference Explains Perceptual Biases for Action Consequences

Abstract

Current theories of predictive processing propose that the brain distinguishes self-generated from externally generated sensory events. Sensory attenuation has been widely considered the mechanism underlying this distinction, as self-generated sensations are often perceived as less intense. However, other studies have reported perceptual enhancement, challenging attenuation-based accounts. Regression toward the mean stimulus intensity may reconcile these seemingly contradictory findings. Here, we tested whether cross-modal interference during action contributes to this regression effect. In a first experiment, 220 healthy participants estimated tone loudness while we manipulated tactile stimulation and movement execution. Cross-modal interference from tactile and proprioceptive signals shifted perceived loudness toward the mean stimulus intensity. In a second experiment, 165 participants judged sound intensity while passively receiving vibro-tactile stimulation of varying strength. Regression toward the mean increased with vibro-tactile stimulation intensity. These findings suggest that cross-modal interference contributes to altered perception of self-generated sensory events.

Introduction

Perceptual neuroscience has long sought to explain why self-generated sensory events are processed differently from externally generated events. It has repeatedly been found that these consequences are perceived as less intense, which has been termed sensory attenuation (Kiepe et al., 2021; Schafer & Marcus, 1973). A dominant account is the forward model, according to which an efference copy of the motor command generates sensory predictions that attenuate expected action consequences (e.g., Dogge et al., 2019; Wolpert et al., 1995). In contrast to this assumption, recent studies have reported enhanced rather than attenuated perception of sensory consequences (Reznik et al., 2015; Thomas et al., 2022; Yon et al., 2018). Bayesian inference provides an alternative framework in which uncertain incoming sensory signals are integrated with prior knowledge about expected stimulation, leading to either an amplification or a reduction in perceived intensity depending on the predicted input (Eckert et al., 2025; Press et al., 2023; Thomas et al., 2022).

We have recently shown that intensity judgments of self-generated auditory stimuli are biased by a regression to the mean sound level (Johnen & Zimmermann, 2025). Specifically, tones quieter than the mean are perceived as louder, whereas tones louder than the mean are perceived as quieter. An earlier study had suggested that sounds near the detection threshold were enhanced while loud tones were attenuated (Reznik et al., 2015). However, our data showed that sounds within the range of levels between 40–70 dB were enhanced, and only sounds louder than 70 dB were attenuated (Johnen & Zimmermann, 2025). The internal representation of the average sound level might be partly determined by short-term experiences, like the current stimulus distribution, but also by long-term exposure to the speaking volume in conversations.

Regression effects in loudness might align the brain’s internal representation of sound intensity with the surrounding acoustic environment. Neural populations encoding sound levels adapt their response properties to maintain efficient processing (Dean et al., 2005). Because humans can discriminate sounds across a roughly 120 dB range despite auditory

nerve neurons encoding only about 30–40 dB, the auditory system must continuously adapt its dynamic range to the current acoustic context and recent sound-level statistics (Dean et al., 2008).

Although regression to the mean might explain the co-occurrence of sensory attenuation and enhancement, it remains unclear why it occurs at all. It can be generated already by simple actions like a button press that produces a tone. Here, we argue that the study of action consequences is confounded by co-occurring sensations like visual and tactile feedback. Perceived intensity judgments from an active condition are usually compared to a baseline condition at rest. However, in this comparison the subtracted variable is not only the action but also the tactile sensation that is produced by pressing the button. Concurrent tactile stimulation may interfere with auditory intensity encoding, thereby increasing uncertainty in auditory representations.

Another confound in the comparison between the active production of a sound and its presentation while the participant is at rest is the predictability of the stimulus. In active button presses, participants can fully predict the temporal presentation of the sound. To control for this confound, EEG studies have used external cues in passive conditions which indicate when the sound will be presented (e.g., Klaffehn et al., 2019). In a previous study, we have used visual cues in passive sound presentations and found a regression to the mean sound level that was indistinguishable from the results in the active condition (Johnen & Zimmermann, 2025). However, although the external cues control for predictability, they - like the tactile sensations in the button press - add a confounding visual sensation. If the simultaneous reception of tactile and auditory stimuli explain sensory attenuation and enhancement, then the action might be irrelevant to observing these effects. In the present study, we tested systematically the influence of the movement and the tactile sensation on the perceived intensity of sounds.

We dissociated movement and tactile feedback to differentiate the contributions of efference-copy-based prediction and cross-modal interference. Furthermore, we tested whether

systematic increases in tactile stimulation strength modulate the magnitude of regression toward the mean.

Research Transparency Statement

General disclosures

Conflicts of interest: All authors declare no conflicts of interest. **Artificial intelligence:** No artificial-intelligence-assisted technologies were used in this research or the creation of this article. **Ethics:** This research received approval from the local ethics board at Heinrich Heine University Düsseldorf, Institute for Experimental Psychology (ZI01_2026_01).

Experiment 1 disclosures

Preregistration: No aspects of this research were preregistered. **Materials:** All study materials are publicly available (https://osf.io/rfg78/files/osfstorage). **Data:** All primary data are publicly available (https://osf.io/rfg78/files/osfstorage). **Analysis scripts:** All analysis scripts are publicly available (https://osf.io/rfg78/files/osfstorage).

Experiment 2 disclosures

Preregistration: No aspects of this research were preregistered. **Materials:** All study materials are publicly available (https://osf.io/rfg78/files/osfstorage). **Data:** All primary data are publicly available (https://osf.io/rfg78/files/osfstorage). **Analysis scripts:** All analysis scripts are publicly available (https://osf.io/rfg78/files/osfstorage).

Method

In total, data of 233 participants were collected. Since 13 participants had to be excluded due to unfittable psychometric functions, we included 220 participants in our analysis (M_{age} = 22.55, SD_{age} = 3.72, 164 female). The sample size was chosen to match that of our earlier study (Johnen & Zimmermann, 2025).

Participants were randomly and equiprobably assigned to one of four conditions. All of them were seated in front of a Dell P2419H Screen with a refresh rate of 60 Hz that was placed 57 cm away from them. The keyboard was placed 30 cm away from the table edge. A motion tracker (Ultraleap Stereo IR 170) was positioned 45 cm away from table edge. After giving their informed consent, the participants received a pseudomized code and participation number. All conditions were built and run in PyCharm Community 2024.3, Python 3.10 (Python Software Foundation, 2024). Used headphones (JBL Tune 500) were connected via cable to the computer. To ensure reliable physical sound levels of the headphones, they were measured by a sound level metre (B&K 2250 by Brüel and Kjær). Every tone was presented for 300 ms with a frequency of 1 kHz. During tone presentation, participants were instructed to keep their gaze directed to a white fixation cross (1° × 1°), presented in the screen center.

In the baseline condition, participants rated which of two presented tones appeared louder. After trial start, the first tone (*probe*), appeared after a random interval between 500 and 3000 ms. The second tone (*reference*), was presented 500 ms later. Probe tones were presented in one out of five possible sound intensities (40, 50, 60, 70 or 80 dB) per trial. Every probe intensity was presented block-wise but in a randomized order for every participant. For each of the five probe intensities, the reference tone was presented in one out of seven possible sound intensities, which were symmetrically centered around the probe intensity with a step size of 2 dB. In the 40 dB condition, the reference tone could have 34, 36, 38, 40, 42, 44 or 46 dB. Each reference tone was repeated ten times in total but randomized across the trials, resulting in a total of 350 trials per session. After the

presentation of the reference tone, participants responded by pressing the left or the right arrow button, which tone they perceived as louder.

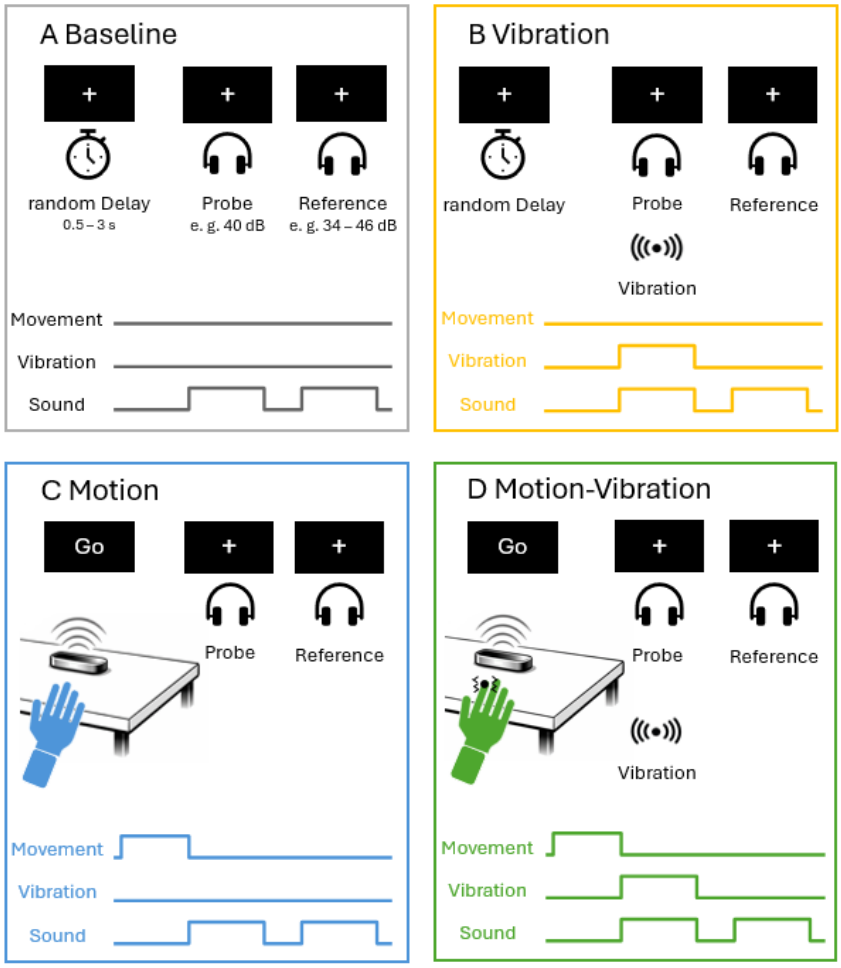
In the vibro-tactile condition, the loudness judgment task remained the same as in the baseline condition. In addition, participants received a vibro-tactile stimulus (Vibrocoin ERM motor, controlled by an Arduino Nano microcontroller ATmega328 operating at 5 Volt) on the right index finger at the same time of the presentation. Similar to the baseline condition, there was the same random delay of 500 to 3000 ms every trial to make the tone and vibration appearance unpredictable.

In the motion condition, participants were instructed to trigger the probe tone themselves. Participants performed a reaching movement above a detection sensor, which triggered the probe tone, as soon as their hand passed the sensor. The reference tone followed again automatically after 500 ms. No tactile feedback was provided at the goal position.

The motion-vibration condition performed the same reaching movement across the motion tracker as participants in the motion condition. In addition, this condition also had a vibrocoin attached to their index finger, which presented a vibro-tactile stimulus simultaneously with the probe tone when reaching the sensor. This condition approximated classic self-generated paradigms in which participants press a button to trigger a tone, thereby combining movement and tactile feedback. Figure 1 illustrates one trial for each tested condition.

Figure 1

Example trial for every condition



Note. **A** Example trial of the baseline condition, in which no movement and vibration was involved. Probe and reference tones appear after a random delay. **B** Identical trial structure for the vibro-tactile condition as for the baseline condition. In addition, a vibration was presented simultaneously with the probe tone. **C** Reaching movement towards motion sensor to trigger probe tone in the motion condition. **D** Identical trial structure as in the motion condition including tactile vibration when reaching final position.

Analysis plan

For every probe intensity and participant, responses for each reference level were analysed within every participant. To these data, a cumulative Gaussian function (see Figure 2A) was fitted. The mean of the psychometric functions served as the point of subjective equality (PSE) between the two presented tones and were interpreted as an index of perceived loudness. For inferential statistics, we had planned to analyze the single-subject PSEs that were subtracted by the physically presented sound level by repeated-measures ANOVAs.

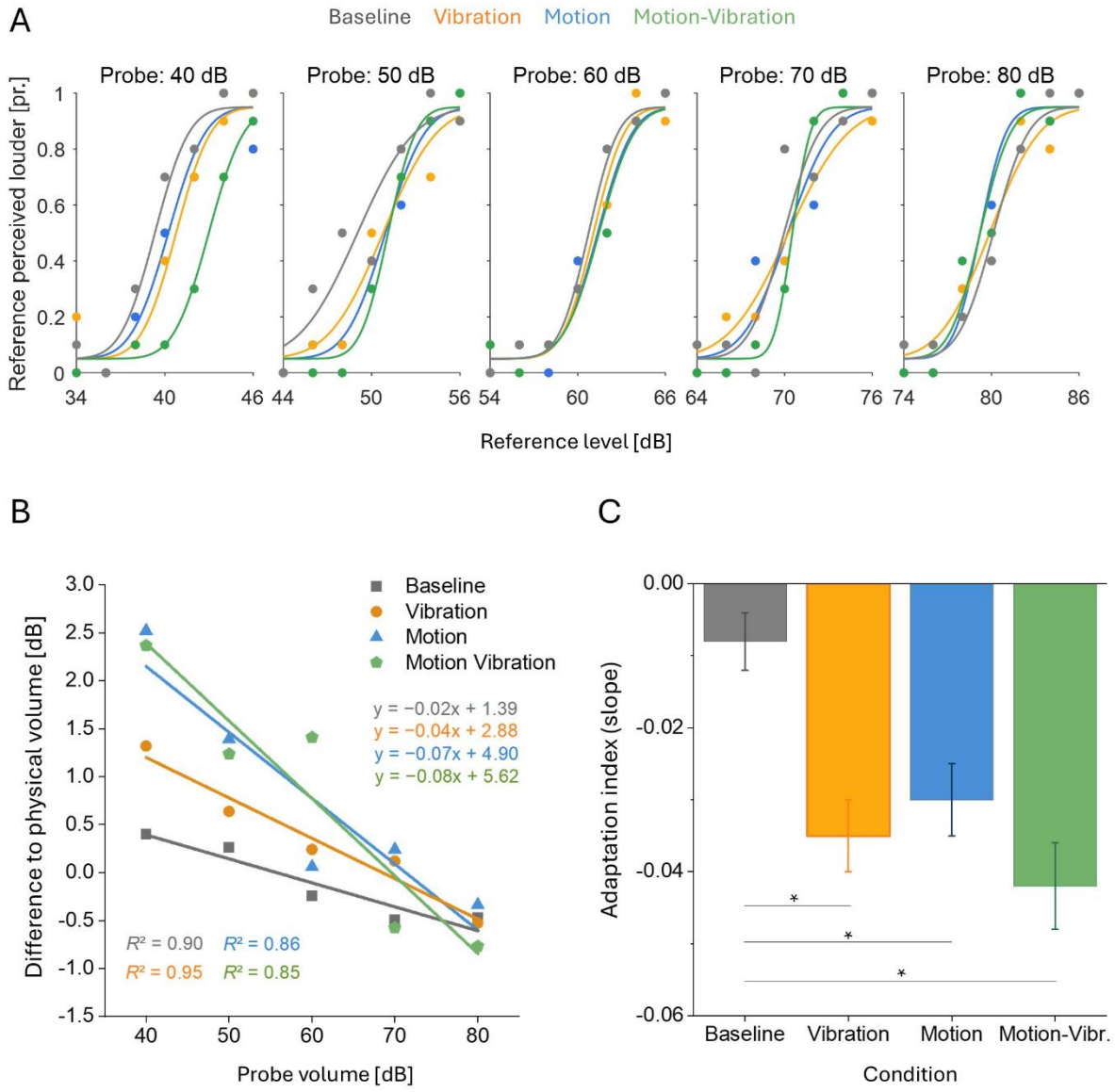
Results

We found a significant effect of loudness perception ($F(4,864) = 52.40$, $p < .001$, $\eta^2 = 0.12$). Quiet tones of e.g. 40 dB were perceived as louder than tones of e.g. 80 dB (see Figure 2A). A significant interaction revealed that loudness perception depends on the condition participants were assigned to ($F(12, 864) = 3.48$, $p < .001$, $\eta^2 = 0.02$). The between-subject factor condition was not significant ($F(3, 216) = 2.25$, $p = .084$, $\eta^2 = 0.01$). Post-hoc Comparisons for adjusted p-values for comparing a family of 10 revealed significant differences between 40 to all other intensities, 50 to all other intensities but not between 60, 70, and 80 dB (all $p > .05$). Figure 2B shows descriptive plots of averaged deviations from the physically presented sound level divided by condition.

We fitted linear regressions for every participant from 40 to 80 dB as index of adaptation-to-the-mean strength. A repeated measures ANOVA revealed significant differences in regression between the conditions ($F(3, 216) = 8.90$, $p < .001$, $\eta^2 = 0.10$). Tukey corrected post-hoc comparisons for a family of 4 revealed significant differences between the baseline and vibration condition ($t = 3.77$, $p_{tukey} = .001$), baseline and motion condition ($t = 3.12$, $p_{tukey} = .011$), as well as baseline and motion-vibration condition ($t = 4.70$, $p_{tukey} < .001$). All other comparisons remained unsignificant. Figure 2C illustrates the averaged slopes separated by condition.

Figure 2

Results of all conditions



Note. **A** Representative psychometric functions for one exemplary participant from each condition and sound level tested. **B** Deviations from physically presented sound intensity as a function of probe level for one exemplary participant from each condition. Lines represent fitted linear regressions. **C** Mean slopes of the linear regressions fitted separately for each participant and experimental condition. Asterisks indicate $p < .05$ for all experimental conditions compared with baseline.

The analyses of the slopes has shown that all experimental conditions differ from the baseline but not from each other. This finding indicates that prediction per se is not necessary to produce the regression to the mean pattern. The vibro-tactile condition received the vibration together with the probe tone, which was after a random delay and showed a significantly stronger regression than the baseline condition. The only difference between the vibro-tactile and baseline condition lies within the presentation of a vibration. This clearly points to the conclusion that diversion of attention is more important for the regression pattern than predictive cues alone. However, predictive cues, especially when presented in another domain than the goal outcome, might also have diverted attention.

Experiment 2

In Experiment 1 we found evidence for a cross-modal interference between the tactile stimulation and the judged loudness of the sound. In Experiment 2 we aimed to test whether regression magnitude scaled with the vibro-tactile stimulation strength. 165 Participants (M_{age} = 23.58, SD_{age} = 6.15, 131 female) performed the same task as in the vibro-tactile condition in Experiment 1. We used three different vibro-tactile stimulation intensities in a between-subject design. Participants in the strongest vibro-tactile stimulation condition received identical vibrations as in Experiment 1, i.e. an average stimulus intensity of 5 V, the medium condition received 50 % of that strength (2.5 V) and the weak condition 25% (1.25 V), while making sure that these 25% were still above participants' perception threshold. After that, participants in all of the three conditions completed the same auditory discrimination 2AFC task with probe intensities between 40 and 80 dB and according reference level in seven intensities varying symmetrically around the probe and being presented ten times each. Participants were requested to not move their hands throughout the entire experiment. Tone and vibration presentation were presented after a random delay of 500 to 3000 ms after trial start without any temporal cue provided.

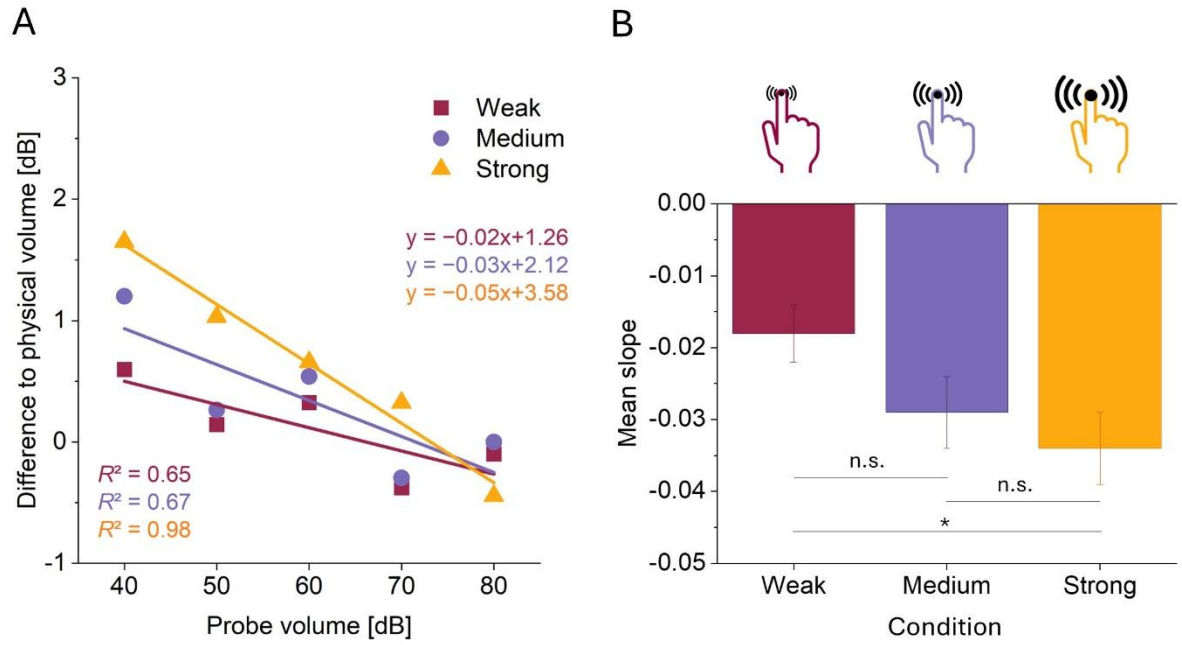
Results

We found a significant effect of sound intensity ($F(4, 648) = 47.55$, $p < .001$, $\eta^2 = .12$). Post-hoc comparisons with an adjusted p-value for a family of ten revealed significant differences of 40 to all other intensities (all $p < .001$) as well as of 50 to all other intensities (all $p < .001$). The main effect of the between-subject factor condition did not reveal significant differences ($F(2, 162) = 0.55$, $p = .576$, $\eta^2 < .01$). The interaction of both factors did not reach significance either ($F(8, 648) = 1.53$, $p = .144$, $\eta^2 = 0.01$). To estimate regression to the mean magnitude, slopes of linear regression fits were determined for each participant (Figure 3A) and analyzed with a repeated measures Anova, which revealed a significant effect of condition ($F(2, 162) = 3.15$, $p = .045$, $\eta^2 = 0.04$). As Figure 3B shows, the slope is steepest in the strong vibro-tactile stimulation condition. Post-hoc comparisons with a p-value adjusted for comparing a family of three revealed significant differences between the strong and the weak condition ($t = -2.46$, $p = .040$), but no difference of the strong to the medium ($t = -0.79$, $p = .712$) or the medium to the weak condition ($t = -1.67$, $p = .219$).

An additional linear regression for stimulation strength revealed that regression slopes became significantly more negative with increasing vibro-tactile stimulation ($b = -0.01$, $t(163) = -2.46$, $p = .015$). Consequently, steeper slopes indicated a greater influence of the tactile signal on auditory judgments, suggesting that the regression to the mean magnitude increases as a function of vibro-tactile stimulus intensity.

Figure 3

Results of all conditions sorted by level of cross-modal interference



Note. **A** Deviations from physically presented sound intensity as a function of probe level for one representative participant from each condition. Lines represent fitted linear regressions. **B** Mean slopes of the linear regressions fitted separately for each participant and conditioned by vibro-tactile stimulation level. Asterisk indicates $p < .05$ for the comparison between the strong and weak vibro-tactile stimulation conditions.

Discussion

In this study, we show that the extent to which auditory loudness estimates regress toward the mean sound level depends on the strength of distracting tactile sensations. Research has investigated the attenuation of self-produced sounds for decades (for a review, see Kiepe et al., 2021). However, we have shown previously that attenuation and enhancement of self-produced sounds result from a regression to the average sound level (Johnen & Zimmermann, 2025). Behavioral findings of regression to the mean sound level are

consistent with electrophysiological recordings that demonstrated adaptive shifts of auditory processing to the average sound intensity (Dean et al., 2005). It is unclear, however, why regression strength should increase when pressing a button. Our present data show that the tactile sensation occurring during the button press induces the regression. We found that the slope of the regression scaled linearly with the magnitude of tactile stimulation. These results offer a novel understanding of why the sensory consequences of our own actions appear different to us.

We systematically studied the relevant factors during a button press that might influence perceived loudness. These are the movement, the tactile stimulation received when touching the button and the temporal predictability of acoustic stimulus occurrence. We first replicated the regression to the mean for self-generated, i.e. predictable stimuli, as reported previously (Johnen & Zimmermann, 2025). The motion-vibration condition served as a proxy for self-generated tones as it includes both a self-initiated movement and the ensuing tactile feedback on the finger, comparable to a button press. In addition, we tested a motion-only condition that did not contain tactile feedback but only the movement. Even without tactile input, we still found a regression of auditory stimuli following an active movement. This may have introduced proprioceptive input that interferes with auditory processing. In sum, we found regression to the mean sound level in the predictable motion and motion-vibration condition, as well as in the unpredictable but vibro-tactile condition. Together, these results do not provide evidence that temporal prediction alone is sufficient to account for the effect. The only common factor across all conditions is the presence of an additional sensation co-occurring with the sound, such as tactile vibration or proprioceptive feedback in the movement-only condition.

There were no significant differences between a predictable, self-generated movement triggering a tone and a randomly presented tone paired with a small vibration on the index finger. Importantly, as shown in Experiment 2, the strength of cross-modal interference mattered: increasing vibration intensity led to steeper regression slopes, indicating a stronger bias in auditory perception. This suggests that diverting attention away from the auditory

modality reduces the precision of auditory perception, which then relies more on prior knowledge. Cross-modal interference might also explain the effect of visual cues that previous studies used to test the role of temporal prediction (Harrison et al., 2021; Johnen & Zimmermann, 2025). Comparable to movement or vibration, visual cues such as a flashing fixation cross or moving bars may draw attention toward the visual modality and away from auditory inputs.

We had previously shown that cross-modal interference determines sensory attenuation for the produced sound while simultaneously the felt intensity of tactile stimulation at the pressing finger increased (Fritz et al., 2022). Cross-modal interference between tactile and auditory sensations has been described previously. Gescheider et al. (1975) already showed that when auditory and tactile stimuli were either in isolation or together, performance only declined for stimuli occurring simultaneously, indicating that how attention is distributed plays a key role in perception. Shared attentional resources between touch and hearing might be provided by the strong functional connections between these systems. The human somatosensory cortex is known to co-activate with auditory regions during the processing of vibrations and texture-related information (Butler et al., 2012; Iguchi et al., 2007; Nordmark et al., 2012; Schürmann et al., 2006). More recently, Convento et al. (2018) found that disrupting activity in primary somatosensory cortex (S1) using TMS impaired auditory frequency discrimination, but only when participants were simultaneously attending to tactile frequency information.

Previous studies traditionally relied on relatively loud tones (>70 dB). In behavioral studies, the findings are rather mixed with only some studies reporting attenuation. In our present and in a previous study (Johnen & Zimmermann, 2025), we found that enhancement effects for tones below 70 dB were stronger than the attenuation effects for the louder tones. In the EEG literature, sensory attenuation has been studied by investigating the suppression of the N1 and the P2 component (Egan et al., 2026; Harrison et al., 2021; Timm et al., 2014). However, it is still unclear how the reductions in these evoked potentials can be related to behavioral results (Giannini et al., 2025). Observed attenuation effects were typically taken

as evidence for a dedicated predictive mechanism. Without accounting for regression-to-the-mean effects, such findings were commonly interpreted in terms of internal forward models of sensory consequences. Our data however challenge the forward model on its major premises. Neither a movement nor predictions are necessary to produce the effect. In addition, in the normal hearing range between 40 and 80 dB enhancement is much more prominent than attenuation.

Instead, our results suggest that cross-modal interference induces uncertainty on the self-produced auditory stimulus. The sensory system might minimize the uncertainty by relying on prior knowledge about loudness. The prior distribution might either be derived by short-term experiences through the stimulus distribution or by long-term experience. In the latter case, the loudness we experience most regularly is the speaking volume, ranging around 60 dB. We assume that the prior is updated constantly through novel acoustic experiences, as has been found in the visual modality (Adams et al., 2004), in time estimations (Jazayeri & Shadlen, 2010) or in sensorimotor learning (Körding & Wolpert, 2004). From this perspective, regression toward the mean can be understood as an adaptive consequence of uncertainty-weighted integration of current input and prior experience.

In conclusion, our results show that the tactile sensation in a button press induces regression to the mean loudness for the produced sound. The finding suggests a novel explanation why the sensory consequences of our own actions appear different to us.

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Research Article

Main Manuscript for

Sensory attenuation reflects proprioceptive recalibration rather than motor forward models

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Abstract

Forward models are widely regarded as the standard framework for predicting and attenuating the sensory consequences of self-generated actions. Sensory attenuation is a prime example, traditionally attributed to efference-copy–based predictions of the tactile consequences of self-touch. Here, we systematically investigated the mechanisms underlying sensory attenuation in 220 participants across six experiments. Using a device that enabled passive hand transport to mimic self-triggered self-touch, we found that passive and self-generated movements produced equivalent levels of sensory attenuation, ruling out the necessity of an efference copy for self-touch perception. Moreover, sensory attenuation occurred only when self-touch was proprioceptively predictable; external predictive cues alone were insufficient. Blindfolding participants did not alter attenuation during passive movements, indicating that visual information is not required. Together, these findings suggest that self-touch perception emerges through multisensory learning that associates spatially congruent limb proprioception with tactile input. We further tested this account by exploiting plasticity of the body schema: when a tactile impulse on the left finger was delivered after the right arm had been passively displaced away from the left hand, sensory attenuation was still observed. These results demonstrate that sensory attenuation arises from learned proprioceptive predictions of self-touch rather than from motor-based forward models.

Keywords: sensory attenuation, proprioceptive prediction, efference copy

Introduction

Human sensory systems are thought to have evolved under strong selective pressure to rapidly and efficiently detect behaviorally relevant events, such as potential threats. Vision and audition primarily signal events at a distance, whereas touch provides information about direct contact with the body. It has been proposed that the brain uses internal models to predict the sensory consequences of self-initiated actions. In the laboratory, the consequences of the prediction can be observed as an attenuation of the according sensory input. If we touch ourselves, the intensity of the tactile sensation appears weaker than if someone else touches us[1].

Two theoretical frameworks compete to explain sensory attenuation. Motor control theory suggests that a forward model receives input from a copy of the motor command, i.e. the efference copy, in order to predict the sensory movement consequences. The physical stimulation will feel attenuated if its spatiotemporal occurrence matches the prediction[1,2]. In active inference, the hierarchical order of inverse and forward model is reversed[3]. Proprioceptive predictions that envisage an effector in a certain future state drive the movement that minimizes the difference between the current and the predicted state[4]. Sensory attenuation thus follows from the deliberate reduction of sensory evidence precision that enables the installment of proprioceptive predictions, which drive movement generation[5]. Self-touch is a special case for this model, as proprioceptive predictions exist in the touching limb, but they might also arise in the bodily location to be touched. In this view, proprioceptive predictions on the location to be touched follow from the selection of a somatosensory target on one's own body. The major difference between both theories is that in motor control theory, an efference copy builds up a forward model whereas in active inference the forward model is computed upstream of movement planning.

Here, we tested both theories against each other, by investigating rigorously the role of the predictive cues in a self-touch paradigm. Sensory attenuation of self-touch is finely tuned to the spatial and temporal structure of action[6,1,7,8,9]. However, explaining sensory attenuation

solely in terms of forward models implies a tight coupling between perceptual intensity and prediction error, an assumption that has been questioned on both theoretical and empirical grounds[5]. Moreover, several studies show that predictions following Bayesian principles might be better suited to explain existing empirical data on sensory attenuation[10,11,12,13,14,15-17,18,19].

We stepwise isolated the different predictive signals and their contribution to sensory attenuation of self-touch. In a series of experiments, we studied the perceived intensity during self-touch. We constructed an experimental device that allowed to perfectly mimic self-generated movements of the right hand which resulted in self-touch of the left hand. One motor passively transported the right arm of participants and a second motor produced a touch experience once the right arm arrived. This helped us differentiate between movement- and prediction-related outcomes.

Results

Self-generated versus *indirectly generated* movements

We studied the felt intensity of tactile intensities for self-touch. An experimental apparatus was custom-built to investigate tactile perception and consisted of a rigid chassis originally designed as a printer frame. The chassis provided a stable, linear guide system along which a movable platform (hereafter referred to as the carrier) could be precisely translated. The carrier was mounted on the chassis and driven by a stepper motor, allowing controlled linear movement along a single axis. Motor control enabled smooth and repeatable positioning of the carrier with high spatial precision. The carrier served as an arm support on which participants rested their right forearm in a comfortable and stable posture. During the experiment, the right index finger was fully extended and oriented toward the direction of motion. The carrier advanced along the chassis until the participant's right index finger made contact with a vertically mounted metal plate positioned at a fixed location along the

movement path. Behind the metal plate, the participant's left hand was positioned such that the left index finger was aligned with the contact location of the right index finger. The mechanical design ensured reproducible movement trajectories and consistent timing of tactile events across trials and participants, making the apparatus suitable for controlled investigations of tactile perception.

Simultaneously with the arrival of the right index finger at the metal plate, the left index finger was tapped by a servo motor, simulating self-touch. After 1000 ms, a second touch was automatically presented to the left index finger and participants had to judge which touch appeared as more intense (Fig. 1A). The first tactile impulse was always presented with 2 N, and the second tactile impulse strength varied according to six adaptive staircase procedures that were measured consecutively within one session. Figure 1B shows average intensity judgments for self-triggered self-touches, subtracted by the baseline performance without any movement (represented by the dashed line). On average, participants reported a reduced felt intensity for the self-produced touch. The analysis revealed a significant effect of time, with an increasing attenuation and differences to the baseline over time ($F(5, 270) = 2.56$, $p = .026$, $\eta^2 = .05$). Comparing the individual time points to the baseline with a *p*-value correction for a testing family of six tests, we find attenuated perception in time points two to six. We sought to examine why attenuation increased over the course of trials. From the continuously tracked hand positions, we calculated movement speed in each trial. We found that participants also moved significantly faster over time ($F(5, 270) = 2.32$, $p = .044$, $\eta^2 = .04$, Fig. 1C), suggesting that they gradually became more familiar with the setup and executed their movements in a more natural, efficient manner.

We then systematically investigated the necessary and sufficient conditions of sensory attenuation. We first wondered whether an efference copy is necessary to induce changes in tactile sensitivity. To this end, we moved the right arm of participants passively. Participants were required to position their right arm on a small carrier with the index finger pointing to the plate. In the *indirectly generated* experiment, participants controlled the carrier via a foot pedal. Participants were instructed explicitly to relax and to not support the indirectly

generated movement by any muscle effort. Simultaneously with the arrival of the right index finger at the plate, a touch was applied on the left index finger. The psychometric measurement followed the procedure that was applied in the *self-generated* experiment. Average intensity estimates are shown in Fig. 1D. Like in the *self-generated* session, all estimates are negative, indicating reductions in the felt intensity of the touch. For *indirectly generated* movements, we did not find any significant effect over time ($F(5, 270) = 0.49$, $p = .781$, $\eta^2 = .01$) and speed, since it was controlled by a motor (Fig. 1E). Since there was no difference over time, the six time points were averaged and afterwards compared to the baseline, which revealed a significant attenuation of the *indirectly generated* triggered touches ($t(54) = -3.62$, $p < .001$, $d = -0.49$, SE = 0.15). An a posteriori Bayesian *t*-test indicates moderate evidence for the null hypothesis ($BF_{10} = 0.19$, error = 0.07) of no difference between the *self-generated* and *indirectly generated* movements. A comparable level of sensory attenuation was found in the *self-* and the *indirectly generated* experiments.

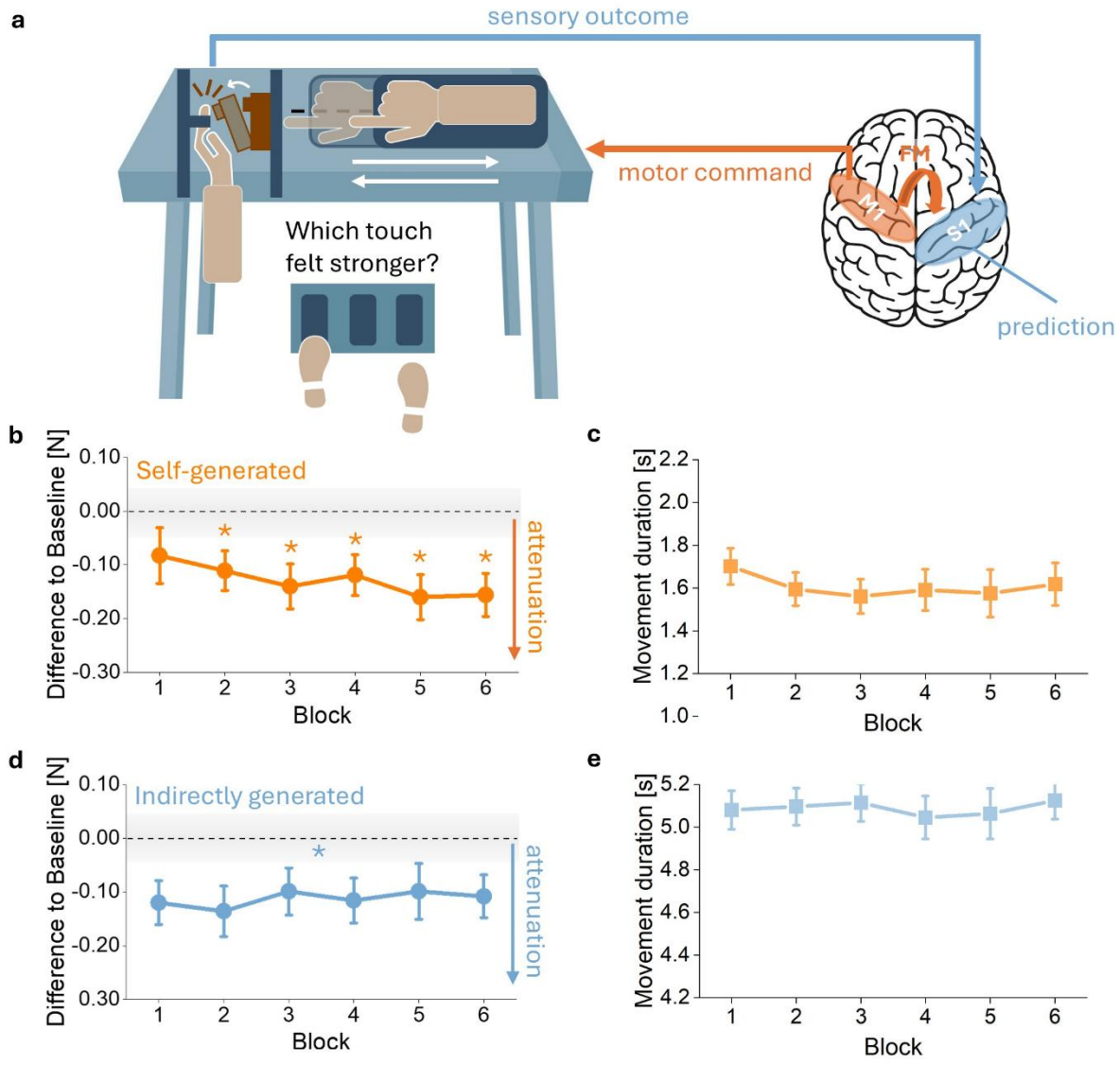

Fig. 1: Methods & materials experiment 1: self-generated versus indirectly generated movement. a Example of a trial, where participants move back and forth. Touches are presented at front position, simulating self-touch. In the *self-generated* experiment, participants move the arm by themselves. In the *indirectly generated* experiment, participants press the middle foot pedal, which starts a motor that moves the arm back and forth. Remaining procedure is identical to *self-generated* session. In the baseline, participants only judge the intensity of two consecutive touches. Right side shows cortical areas involved in movement and prediction to underline the two main approaches in research: forward model versus prediction. **b** Average tactile intensity estimates relative to baseline in the *self-generated* experiment, **c** shows the mean movement duration towards the plate to trigger

self-touch. **d** Average tactile intensity estimates relative to baseline in the *indirectly generated* experiment. Black dashed line indicates baseline estimates. **e** Mean movement duration towards the plate to trigger self-touch in *indirectly generated* experiment. Error bars represent S.E.M. for all experiments. Asterisks indicate significant differences.

Movement speed does not affect sensory attenuation magnitude

We then investigated the movement speed of the *self-generated* experiment that differed across the measured time points (see Fig. 1CE). We ran the *indirectly generated* experiment over a long distance driven at slow speed (5 cm with 1 cm/s, *long-slow*). In addition, a shorter distance of 0.5 cm and a faster speed of 3 cm/s (*short-fast*) were tested to check for differences between these two conditions. Estimates were compared against judgments from a neutral baseline condition.

A repeated measures ANOVA for the 50% threshold-PSEs (points of subjective equality) for all conducted psychometric functions revealed a significant effect of tested condition ($F(2, 108) = 6.24$, $p = .003$, $\eta^2 = 0.10$). Post-hoc comparisons with an adjusted p-value for comparing a family of three revealed a significant attenuation for the *short-fast* condition compared to the baseline ($MD = -0.04$, $SE = 0.02$, $t = -2.55$, $p_{holm} = .024$), of the *long-slow* condition compared to the baseline ($MD = -0.05$, $SE = 0.02$, $t = -3.39$, $p_{holm} = .003$), but not between the *short-fast* and *long-slow* condition ($MD = 0.01$, $SE = 0.02$, $t = 0.84$, $p_{holm} = .402$). All conditions that included a movement of the right arm led to a significantly attenuated perception compared to the baseline.

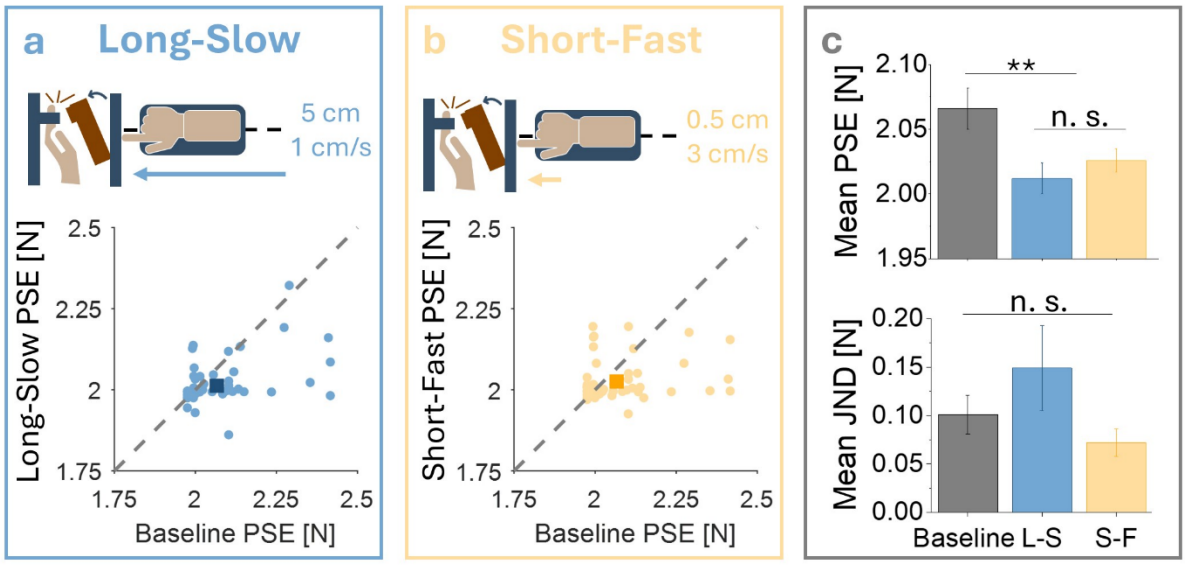

Fig. 2: Movement dynamics that lead to attenuated perception. a Illustration of *long-slow* movement until touches are presented, identical movement as in the *indirectly generated* experiment of before. Light blue data points show tactile intensity estimates from all participants. The dark blue square shows the mean**. b** Visualization of fast movement 0.5 cm back and forth. Yellow dots in the scatter plot show single subject data. The orange square shows the mean. **c** Bar graphs for mean PSE and JND (just noticeable difference) for all tested conditions. Error bars represent S.E.M. for both experiments.

n. s. = not significant, L-S = Long-Slow, S-F = Short-Fast, ** $p < .01$

Movement control is not necessary for sensory attenuation

We aimed to fully exclude any control that participants had over the passive movement. In the *indirectly generated* experiment, participants pressed the foot pedal to start the motor that transported the arm. Although the arm movement was passive, participants still had control over the start of the movement. In the *externally generated* experiment, the experimenter was in control of steering the motor which drove the participants' arm to induce the touch on the left finger. They only pressed the foot pedal to enter their responses but

could not steer the motor anymore (Fig. 3A). When comparing tactile intensity estimates collected in the *externally generated movement* experiment to a separately measured baseline, we found significant attenuation ($t(54) = 2.99$, $p = .004$, $d = .17$). A repeated measures ANOVA for the factor time again did not reveal any significant effect ($F(5, 270) = 0.59$, $p = .708$, $\eta^2 = .01$). For every time point collected, participants perceived the presented touches less strong than in the non-moving baseline.

To compare the amount of sensory attenuation in the *externally* to the *indirectly generated* experiment, we calculated the differences of both experiments to the baselines and performed a repeated measures ANOVA with the factors generation type and time point. Since the predictability was comparable in both experiments, we expected a similar strong attenuation between an *externally* and *indirectly generated* movement experiment (Fig. 3B). As the analysis revealed, the *external* experiment did not differ concerning the attenuation from the *indirectly generated* experiment, $F(1, 54) = 0.06$, $p = .802$, $\eta^2 < .01$. As expected, the time point of measurement also did not yield any significant difference ($F(5, 270) = 0.74$, $p = .591$, $\eta^2 < .01$). An additional Bayesian ANOVA was run and revealed moderate evidence in favor of the similarity assumption between the *externally* and *indirectly generated* movement experiment ($BF_{10} = 0.16$, error % = 34.73). Strong evidence was given for the absence of a time course ($BF_{10} = 0.01$, error % = 0.58).

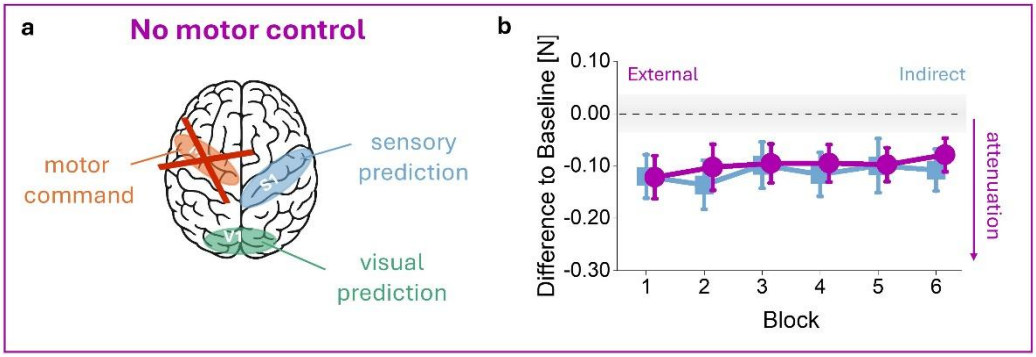

Fig. 3: External motor control causes attenuated perception. a Cortical areas involved in *externally generated* movement. **b** Blue line represents the attenuation in the *indirectly generated* experiment, magenta represents the *external* experiment. Shown are trials 1 to 120 after calibration. Black dashed line indicates baseline estimates. Error bars represent S.E.M.

Predictability

The results of previous experiments show that neither an efference copy nor control over the movement are necessary for sensory attenuation to occur. Next, we examined the role of predictability. Participants had multiple possibilities to predict the appearance of touches on the left index finger.

First, they were able to see their right arm moving towards the plate and they could visibly predict the moment of the arm reaching its final position of touch presentation. Second, the touch appearance was always temporally predictable. Either the movement was actively executed by the participants themselves or the motor drove their arm with the exact same speed and duration every trial. Third, their proprioceptive perception of the right arm might have made it possible to predict at which arm position the touches will be presented. They were able to feel their right arm moving into the direction of the left hand, which inevitably leads to a proprioceptive prediction. In experiments 4-6, these components will be

investigated individually to find the final determining factor that is crucial in the appearance of tactile sensory attenuation.

Visual predictability

The prediction of where and when self-touch occurs has previously been thought to depend on the efference copy. However, we found predictive sensory attenuation in the absence of a self-generated movement. Instead of a top-down signal linked to movement control, the prediction must derive from a sensory signal which informs about when the right arm touches the left finger. Such a signal might stem either from the visual or the proprioceptive sense.

We first tested whether a visual signal would be sufficient to produce sensory attenuation. A LED was placed directly next to the touched finger to match the target position (*congruent*) and another LED was placed in the periphery behind the right (resting) arm to create a non-match (*incongruent*, Fig. 4A). In each trial, one of the LEDs lit up and participants were instructed to direct their gaze to the lit LED. 500 ms later, the first touch was presented. Consequently, in the spatial *congruency* condition, participants were always watching their own finger being touched and keeping their focus there, while in the spatial *incongruency* condition the touch was not visually observable. The order of the LEDs lighting up was randomized across trials.

In a repeated measures ANOVA, we found no significant difference between the cued conditions and a neutral baseline ($F(2, 108) = 2.36$, $p = .099$, $\eta^2 = 0.04$, Fig. 4B). A follow-up Bayesian paired samples *t*-test also provided moderate evidence in favor of no difference between the *congruent* and the *incongruent* LED cued conditions ($BF_{10} = 0.15$, error % = 0.08). Neither visual temporal cueing alone, nor visual spatio-temporal cueing is a sufficient prediction to attenuate the perception of tactile stimuli.

We then tested whether vision was necessary at all to observe sensory attenuation. We ran the *indirectly generated* experiment and blind-folded participants (Fig. 4C). The comparison

with the baseline revealed again a significantly attenuated perception of the *blind* experiment ($t(54) = 3.12$, $p = .003$, $d = 0.42$). Even when blinded, participants still perceived the presented touches less intense when their arm was being moved towards the touched finger compared to a non-moving baseline. A repeated measures ANOVA for the factor time did not reveal any significant effect ($F(5, 270) = 0.84$, $p = .519$, $\eta^2 = .02$). A posteriori, another comparison between the seeing *indirectly generated* and the *blind* experiment was conducted with no difference found, $F(1, 54) = 0.02$, $p = .881$, $\eta^2 < .01$ (Fig. 4D). Comparable to previous conditions, an additional Bayesian repeated measures Anova was performed to test for similarity between the *blind* and the *indirectly generated* experiment, which was given with moderate evidence ($BF_{10} = 0.13$, error % = 59.27).

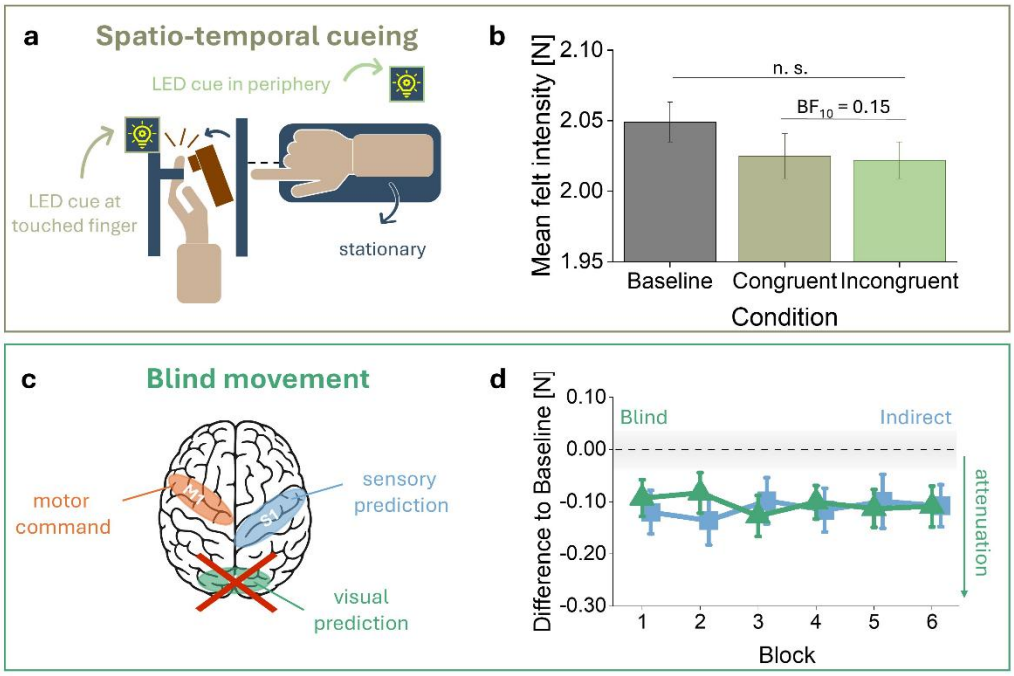

Fig. 4: No influence of visual and temporal predictability on tactile attenuation. a Illustration of the setup testing the effect of spatially *congruent* and *incongruent* visual cuing on tactile intensity estimates. **b** Average tactile intensity estimates for the baseline, the spatial *congruency* and the *incongruency* condition. **c** Illustration of putative cortical contribution to results in the *blind* experiment. **d** Average tactile intensity estimates in the

blind experiment (shown in green) and in the *indirectly generated* experiment (shown in blue). Black dashed line indicates baseline estimates. Error bars represent S.E.M. in all experiments, n. s. = not significant.

Proprioceptive (un-)predictability

In every experiment in which we found attenuation, the right arm was moved towards the metal plate which ended in a touch on the left index finger. Visual prediction was removed and participants still reported attenuation. Thus, sensory attenuation for passively induced self-touches might derive from two sources. First, the mere movement of the right arm, irrespective of its direction, is sufficient to decrease the felt intensity of the touch in the left finger. Second, the continuous proprioceptive predictability of the touch through the movement of the right arm might yield sensory attenuation.

We aimed to dissociate the two putative influences on the perceived tactile intensity by presenting touches on the left finger randomly with respect to the right arm movement. The experiments contained four different time points at which touches were presented, which were randomized across trials (Fig. 5A).

Touches could appear *randomized* during movements, i.e. i) when the arm approached the metal plate or ii) when it receded from it or iii) at the time when it changed direction after receding or iv) when the arm touched the metal plate. When a trial started, no cue indicated when the touch would appear. If every arm movement results in attenuation of tactile impulses on the left index finger, the effect should be present for stimulations at all time points.

As a repeated measures ANOVA revealed, there are neither differences between any of the tested positions ($F(3, 132) = 0.31$, $p = .818$, $\eta^2 < .01$), nor differences to a separately measured baseline ($F(4, 216) = 0.79$, $p = .533$, $\eta^2 = .01$, see Fig. 5B). Even though the

movement was identical to previous experiments, the perception of the presented touches changed in this one. The timing of the touch appears to play the determining role; without an ending arm position as cue, attenuation was no longer observed. An additional Bayesian repeated-measures ANOVA to test for the absence of differences between positions provided strong evidence for the null hypothesis (BF_{10} = 0.03, error % = 0.66, Fig. 5C), indicating that all positions led to comparable touch perception. A mere movement of the right arm itself is not sufficient to cause attenuation, leaving the factor proprioceptive prediction as the main cause of this phenomenon.

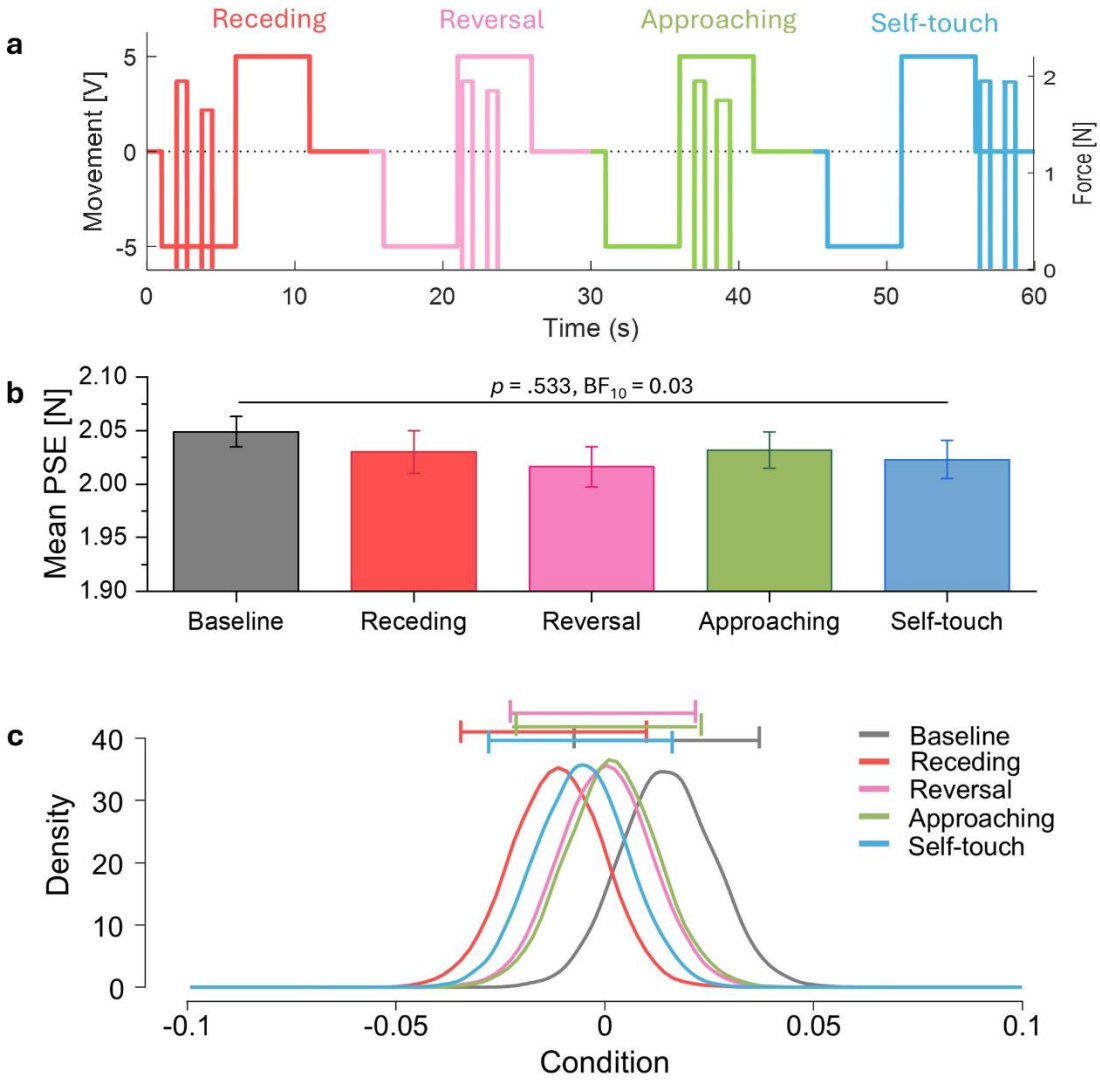

Fig. 5: Randomization of position for proprioceptive unpredictability. a Position of the right arm passively moved by the stepper motor shown by the continuous line. Vertical bars indicate the time of the presentation of the tactile probe and the comparison stimuli. **b** Bar graphs show non-significant differences in the PSE between the positions. Error bars represent S.E.M. **c** Model-averaged posterior distributions of the Bayesian Anova.

Proprioceptive recalibration

Our experiments singled out proprioception as the necessary signal for sensory attenuation of self-touch. Proprioception continuously informs about movement direction and the final limb positions at the time of self-touch. We wondered whether both, movement direction and final arm position are necessary to cause sensory attenuation. To disentangle the influence of both, in the *proprioceptive recalibration* experiment, the right arm was passively transported in the opposite direction (Fig. 6A). In the current experiment, participant's hands were moved 5 cm backwards, i.e. away from the left hand, for 90 trials, while the first touch was delivered immediately upon reaching the reversal point, which served as recalibrated position for self-touch. A paired samples *t*-test of the *recalibrated* experiment was conducted to compare the effects to a separately measured baseline. Touch perception was significantly attenuated ($t(54) = 3.20$, $p = .002$, $d = 0.43$, SE = 0.13), even though their arms were 5 cm apart.

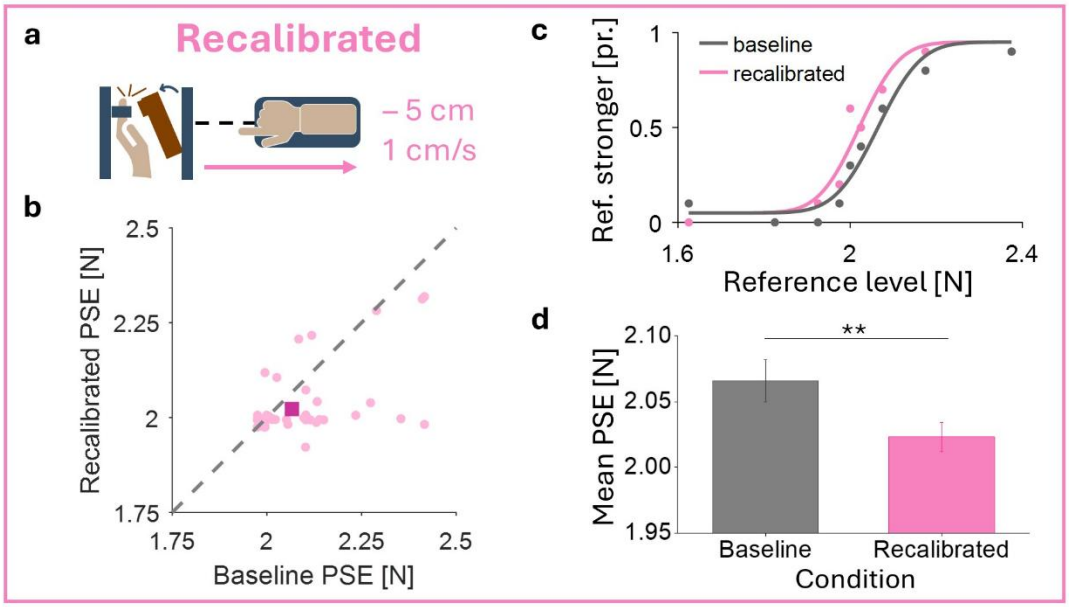

Fig. 6: Recalibration of self-touch. a Backward moving experiment, where touches are presented at the *recalibrated* position. **b** Light pink dots are single subject data, dark purple shows the mean. **c** Representative psychometric function for one participant, baseline and *recalibrated* experiment. **d** Bar graphs for mean the PSE for the baseline and recalibrated self-touch. Error bars represent S.E.M.

Discussion

We investigated the necessary and sufficient factors for sensory attenuation during self-touch by isolating each signal that predicts the resulting tactile sensation (Fig. 7B). In our experimental setup, the dynamics of *self-* and *externally* generated movements were closely matched, differing only in movement speed. As long as predictability about the upcoming tactile stimulation was provided, apparent self-touch led to sensory attenuation. In the *self-generated* experiment predictability was made available through the movement intention and in the *indirectly generated* experiment through the repeated exposure (Fig. 7A). Sensory attenuation in predictable passive movements demonstrates that an efference copy signal is

not necessary to induce sensory attenuation. Our results directly challenge the prevalent explanation involving a forward model architecture[20,1].

a

	Self-generated	Movement	Control	Temp. Pred.	Visual Pred.	Proprio. Pred.	Goal-direction	Attenuation
Self-generated	✓	✓	✓	✓	✓	✓	✓	✓
Indirectly generated	✓	✓	✓	✓	✓	✓	✓	✓
Externally generated	✗	✓	✗	✓	✓	✓	✓	✓
Cued	✗	✗	✗	✓	✓	✓	✗	✗
Blind	✗	✓	✓	✓	✗	✓	✓	✓
Random	✗	✓	✗	✗	✗	✗	✗	✗
Recalibrated	✗	✓	✗	✓	✓	✓	✓	✓

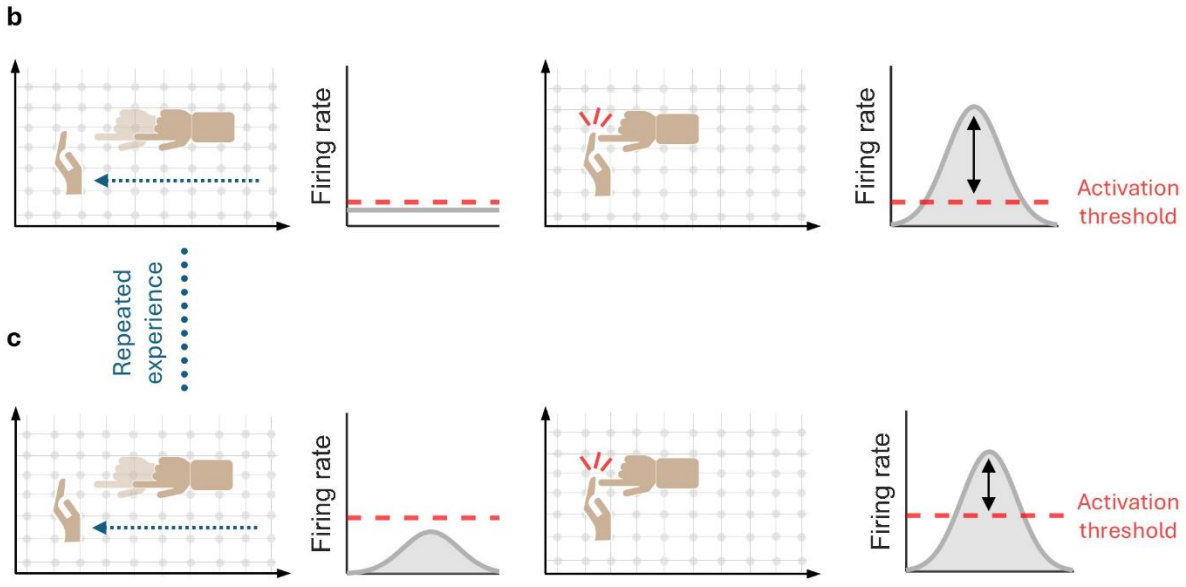

Fig. 7: Emergence of attenuated perception. a Factors (columns) potentially influencing sensory attenuation and their contribution. A tick indicates that the factor was present in the experiment (rows), a cross indicates that the factor was excluded. Pale ticks indicate indirect involvement of the factor in the experiment. **b** First-time performance of self-touch without preactivated threshold. **c** Evoked response of somatosensory after experiencing repeated

self-touch, which builds up prediction.

Pred. = predictability.

Instead, our findings suggest that sensory attenuation is the signature of a mechanism that detects self-touch based on the congruency of proprioceptive signals across the limbs. The concurrent experience of spatially congruent proprioceptive signals giving rise to a tactile sensation may establish a learned prediction of self-touch. In active inference, proprioceptive predictions initiate movements with the aim to minimize the proprioceptive prediction error[4]. In the special case of self-touch, two proprioceptive predictions co-exist, one in the limb that is touching and one in the to be touched location. Sensory attenuation of self-touch is the consequence of the prediction error at the to be touched location. Predicted self-touch in the to be stimulated limb may raise the baseline activity of somatosensory neurons so that the evoked response to the actual touch is reduced, resulting in sensory attenuation (Fig. 7B). Neurally, the prediction of self-touch might be implemented in neurons that encode limb position using population codes and gain-field interactions, allowing the relative position of the two hands to be represented implicitly within a shared body-centered reference frame[21,22].

We also show that proprioceptive predictions can be learned to result in self-touch at a remapped position. When the right arm was repeatedly moved to a position 5 cm from the left hand, paired with tactile stimulation of the left hand, sensory attenuation was observed. In the proprioceptive *recalibration* experiment, no tactile feedback was delivered to the right arm, as participants no longer touched the metal plate, unlike in the previous experiments where sensory attenuation was observed. Trial conditions were exactly identical to one of the four presentation positions from the *randomized* experiment except for predictability: in the *recalibration* experiment, position and timing were predictable and associated with self-touch, whereas in the *randomized* experiment neither the position nor the timing of the touch was

known at trial start. In all experiments showing attenuated perception including the *recalibration* experiment, participants had the opportunity to learn the association between a specific arm position and the subsequent touches on the left finger. This suggests that the right moving arm serves as a natural cue for the tactile stimulus on the left finger. Attenuation of perception occurs only when this cue reliably predicts the sensory outcome; without such a cue, perceptual responses are indistinguishable from those in the non-moving baseline. This arm position does not have to be naturally goal-directed or semantically related but can be recalibrated. Such plasticity of the body schema has been studied in the well-known rubber hand illusion[23,24,25].

In the non-visual rubber hand paradigm, the experimenter guides the participant to stimulate her unseen fake hand, while at the same time the physical hand is stimulated[26]. In consequence, proprioception drifts to the position of the fake hand. Consistent with the idea that self-touch is predicted via proprioception, we previously reported stronger sensory attenuation at the location where participants expected their hand to be than at its actual physical location[27]. The rubber hand illusion can alter the perceived position of the touching hand, but sensory attenuation persists despite this proprioceptive displacement[20]. In our *recalibrated* experiment, participants experienced a tactile sensation only in the left hand, while in actual self-touch, both hands are stimulated. However, studies have shown that after learning to perform self-touch without tactile stimulation on the touching finger, sensory attenuation still occurs[6].

Our data allow us to infer which sensory signals are necessary to predict the experience of touch. A spatiotemporal visual cue at a *congruent* position alone does not lead to sensory attenuation. In contrast, predictive proprioceptive signals reliably induce attenuation, suggesting that it is not the mere detection of touch, but specifically the detection of self-touch, that is functionally relevant for the sensory system. Unpredictable self-touches through movements of the right arm did not yield any changes in tactile perception, ruling out that

sensory attenuation might be explained through a gating mechanism initiated by the movement of the right arm and being transferred to the left index finger[28].

One previous study directly compared sensory attenuation of self-touch in an active and a passive condition[29]. In that study sensory attenuation was significantly stronger in the self-generated condition. A right index finger was resting on a plate which was suddenly removed such that the right index finger fell on the left index finger. We assume that the surprise of the passive finger movement might have affected their data.

In conclusion, we found that sensory attenuation is the consequence of proprioceptive predictions. The existence of proprioceptive predictions at the touched body location explain sensory attenuation in *self-* and *indirectly generated*, *movement speed*, *external*, *blind*, and *recalibrated* experiments. Sensory attenuation is not based on an efference copy or a movement planning as previously thought. Our data suggest that a multisensory learning of spatially congruent limb proprioception paired with a tactile sensation leads to the emergence of self-touch perception.

Methods

Material

Touches were delivered on the left index finger of participants by a wooden rod (3 x 0.5 x 0.5) that was attached to a servo motor (Savöx SC-1257 TG), controlled by an Arduino nano V3.1. In the beginning, there was a distance of 2 cm between the wooden rod and the touched finger. A stepper motor (Wantai stepper motor 42BYGHW 609) moved the right arm on a carrier back and forth along a chassis (Conucon, Hamburg, Germany) in the passive moving experiments, controlled by a separate Arduino nano V3.1.
We used an HTC tracker (3.0) that was installed on the wooden carrier to track the position of the right arm for the *self-generated*, *indirectly generated*, *external* and *blind* experiments. The carrier was 21.6 x 21.6 cm and carried another wooden plank of 21.6 x 5.1 cm. At the

front of the wooden plank, a wooden handle of 9 x 4 cm was placed that participants grabbed with their right hand to rest their index finger on it. In a few calibration trials in the beginning, the exact positions of touching the plate as well as 5 cm away from it were calibrated. Unreal Engine (v. 4.26) was used, running on a Windows 10 desktop computer (Alienware Aurora R8, Intel Core i7 8700 @3.2 GHz, 16 GB RAM, NVIDIA GeForce RTX 2080 graphics card), with the virtual environment using SteamVR (v. 1.25.3) and the SteamVR 2.0 tracking system. In the *self-generated* experiment, the first 20 trials were used for calibration and to accustom the participants to the setup and the movement that they were asked to perform. Used headphones were Soundcore Life Q30 (A3028), the foot pedal was an USB Triple Action Foot Switch FS3-P by Garmade.

In the *movement speed*, *randomization*, *spatiotemporal predictability*, and *recalibration* experiments VR equipment was no longer necessary, since these experiments were programmed and run in PyCharm 2024.3 and Python 3.13. The Arduino and motor remained the same. Participants were in the beginning positioned while touching the plate and the distances were completely driven by the pre-defined distances in the PyCharm 2024.3 script.

Self-generated versus indirectly generated movement

The sample size was based on the results of a piloting study (https://doi.org/10.17605/OSF.IO/QFTVJ), which suggested 55 participants for our repeated-measurement design with three separate experiments. In total, 59 participants took part in the experiments. Since four of them did not meet our inclusion criteria of answering within a certain range, we had to exclude them. Finally, 55 participants (M_{age} = 28.42, SD_{age} = 12.14, 39 female) completed a baseline measurement as well as an *self-generated* and *indirectly generated* experiment.

In the baseline, participants were instructed to rest their right arm on the carrier so that their stretched out right index finger could touch the metal plate (see Fig. 1A). The left hand was placed on the other side of the plate so that the left index finger was fixated in a velcro fastener. During the baseline measurement, the right arm did not move. On the left index finger, two touches with a delay of 1000 ms were applied and participants had the task to decide which touch was stronger. In the *self-generated* experiment, participants were instructed to move their arm including the carrier back and forth with a distance of 5 cm. When the participants' arm arrived at the reversal position, a tone (500 Hz, 300 ms) was played to signal the change of direction. In the *indirectly generated* experiment, the movement was generated by the stepper motor and participants were explicitly told to not resist or help the motor movement. They were instructed to initiate the motor movement by pressing the middle foot pedal (Fig. 1A) whenever they arrived at the reversal position, which was again signaled by a tone.

The baseline lasted 20 trials, while the *self-generated* and *indirectly generated* experiments each lasted 140 trials, divided into seven different sets of 20 trials in order to investigate the time course. A 20-trial adaptive Robbins-Monro algorithm, operating between a minimum of 0.5 and a maximum of 3.5 N, was used to detect the sensory threshold for each participant. The intensity of the first touch (probe) always remained the same (2 N), while the second touch (reference) changed in its intensity depending on the answer of the participant. Threshold estimates were defined as the intensity levels reached by the adaptive staircase procedure in the final trial of each of the six blocks. After reaching the final trial in each of the six blocks, the adaptive staircase algorithm was reset. Responses were recorded using a foot pedal. The assignment of pedals was counterbalanced: for half of the participants, the left pedal indicated the first touch and the right pedal the second, while for the other half the mapping was reversed. Participants wore headphones, which also played a tone after participants responded with the foot pedal to signal the start of the next trial. Participants were instructed to answer with an unseeded response which of the two touches felt more intense (two-alternative-forced-choice-task).

The first trials of the *self-generated* and *indirectly generated* experiment were used to calibrate and accustom the participants with the setup. These trials were not included in the analysis. In between the experiments, participants could take a break. The order of the experiments was randomized across participants. Within participants, the experimental trials were presented block wise.

External control

We collected a new sample of 55 participants after one exclusion due to technical issues of calibrating the VR environment reliably with the hand tracker (M_{age} = 22.24, SD_{age} = 2.63, 46 female) to meet the same sample size as in the *self-* and *indirectly generated* experiments. Baseline and experimental trials were identical to the *indirectly generated* experiment, except that the experimenter, and not the participants, had control over the start of the passive hand transport. All participants had to undergo a new identical baseline measurement. In the *external* experiment, participants had no control over the stepper motor that moved their arm (Fig. 3A). At the start of each trial, the experimenter initiated the motor movement. A tone was presented after the response was provided by the participants as well as when arriving at the reversal position to indicate the start of the movement towards the left finger.

Blind predictability

In the *blind* experiment, participants completed the same task as in the *indirectly generated* experiment. In both, the baseline and the experimental trials, participants were blindfolded (Fig. 4B). The sample was identical to the *external* movement control experiment. Participants could decide when to press the middle foot pedal (Fig. 1A) to have their arm passively moved.

Movement speed

We collected data of 58 participants and included 55 in our analyses (M_{age} = 23.17, SD_{age} = 3.95, 48 female). For greater precision, psychometric functions were measured by presenting constant stimuli with 9 possible reference levels (1.6 and 2.4 N, in equiprobable steps) with 360 trials in total. The reference levels (second touch) were symmetrically distributed around the probe level (first touch) of 2 N, with step sizes increasing toward the extremes from 0.025 to 0.175 to 0.375 N. Three participants were excluded because their psychometric functions could not be reliably fitted.

Two conditions varying in distance and speed were included just like an additional baseline measurement. In the first condition, movements were *short-fast*, in the second *long-slow* (Fig. 2A-B). The baseline measurement had a random delay between 500 and 3,000 ms. In all conditions, trial start was cued by a signal tone. In the *short-fast* condition, the right arm was driven back and forth 0.5 cm at a speed of 3 cm/s. Simultaneously with the arrival of the participant's hand at the plate, the first touch was applied. The second touch appeared after 1000 ms. The *long-slow* condition had the same distance and speed as in the first experiments (5 cm at 1 cm/s). The remaining procedure stayed the same. The order of the conditions was randomized while the trials themselves within a condition were presented block wise. After half of the trials participants could take a break.

Recalibration

The sample of the *recalibration* experiment was the same as in the movement speed experiment. After having tested movement speed and duration, the direction was investigated too. In the *recalibration* experiment, the right arm was transported away from the left hand (Fig. 6A) to recalibrate the self-touch position. In the *recalibration* experiment, participants drove 5 cm back and received the touches when the arm arrived at the reversal position that served as recalibrated final self-touch position. After participants responded,

their right arm was automatically transported back to the plate after which a new trial started. No visual or physical cue indicated the recalibrated position, i.e. participants could not visually predict when they would reach the target position for the touches.

Randomization

We collected data of 59 people and included 55 in our analyses (M_{age} = 23.17, SD_{age} = 3.95, 48 female). Four participants were excluded because their psychometric functions could not be reliably fitted in all measured positions.

Next to a baseline measurement, we ran experimental trials in which touches appeared at four possible positions relative to arm movement, *randomized* across trials. Participants could thus not predict when a touch would occur. Two of the positions were identical to the ones from the *external* self-touch and *recalibrated* experiments. Additionally, touches could be presented at any random position during the movement backward or forward. Speed and total distance were identical to previous experiments (5 cm with 1 cm/s) and remained the same in every trial. We used psychometric functions for every touch presentation position with a probe level of 2 N and nine different reference levels between 1.6 and 2.4 N that were each presented ten times.

Visual spatio-temporal predictability

The visual spatio-temporal experiment was tested with the same sample as the *randomized* experiment. Since this experiment did not include any passive or active movement, the servo motor was not needed for this setup. Instead, one segment of a standard SMD LED strip (GOMING, 1.7 x 0.8 x 0.3 cm, approx. 30 lm, viewing angle 120°) was attached either 0.5 cm behind the touched finger (*congruent*) or far behind the resting right arm (*incongruent*), 60 cm away from the participant's position, 42 cm away from the carrier, and 55 cm away from the touched finger, to direct the participants' view away from the touch presentation. At trial start,

one of the LEDs lit up and 500 ms later a touch was applied on the left index finger. After the second touch had appeared 1000 ms later, participants provided their response with the foot pedal. Which LED lit up was randomized within participants. For each LED position, separate psychometric functions were measured using identical reference levels and step sizes as in the previous experiments. The right arm remained stationary for the whole duration of the experiment while touching the metal plate with the right index finger. After half of the trials participants could take a break.

Author contributions

Conceptualization, S.J., M.B., E.Z..; methodology, S.J., M.B., E.Z.; software, M.B. and S.J.; analysis, S.J. and M.B.; resources, E.Z.; data curation, S.J. and M.B.; writing—original draft, S.J. and E.Z.; writing—review & editing, S.J., M.B. and E.Z.; visualization, S.J.; supervision, E.Z., project administration, E.Z.

Declaration of interests

The authors declare no competing interests

Declaration of generative AI and AI-assisted technologies

During the preparation of this work, the authors used ChatGPT (OpenAI) to assist with language polishing and editorial improvements. All scientific content, interpretations, and conclusions were developed by the authors, who reviewed and take full responsibility for the final manuscript.

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