

**Spatial and temporal specificity of sensory attenuation in the
tactile and auditory modalities**

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List of abbreviations

CNScentral nervous system
EEG electroencephalography
ERPevent-related potential
JNDJust Noticeable Difference
MEG magnetoencephalography
MEPs motor-evoked potentials
OCD obsessive-compulsive disorder

PD Parkinson's disease
PSEPoint of Subjective Equality
SA sensory attenuation
SMAsupplementary motor area
TMS ...Transcranial Magnetic Stimulation
VRvirtual reality

Summary

The brain differentiates self-generated sensations from those originating in the external world. To prioritize and efficiently process sensory information, self-generated stimuli are attenuated compared to externally generated stimuli. This phenomenon known as sensory attenuation has been shown for the tactile, auditory, and visual modalities. This dissertation aims to contribute to further investigate the effects of sensory attenuation effects in the tactile and auditory modalities. Three empirical studies were conducted.

In Study 1, we showed that during self-touch, proprioceptive information from the touched body-part is neglected when visual information about the event is available. Contrary, when the visual signal is absent, attenuation effects are only observed when proprioceptive information related to the touching and the touched body-part match.

Study 2 aimed to replicate and prolong a temporal recalibration effect for tactile attenuation for self-touch. A previous study demonstrated that sensory attenuation for self-touch can shift in time. As we were not able to show such shift, we conclude that sensory attenuation for self-touch is less flexible to temporally adapt than previously assumed.

Study 3 demonstrated a tactile enhancement effect for the moving hand during a goal-directed button-press movement. We hypothesized that attention shifts towards the tactile modality during such target-oriented movements. Due to the functional connectivity of the auditory and tactile modalities, we expected to observe a reduction in attentional resources within the auditory modality. We found sensory attenuation for sounds in the presence of tactile feedback during the button press. We propose that attentional shifts towards the tactile modality during goal-directed movements lead to sensory attenuation effects in the auditory domain.

With the results of the three studies presented in this dissertation, we were able to contribute to further examine the temporal and spatial specificity of sensory attenuation within the tactile and auditory modalities.

1 General Introduction

1.1 Self and externally generated stimuli

In the course of shifting gaze from one point to another, ocular motion induces considerable shifts in visual input upon the retina. These alterations are registered by retinal photoreceptors as the visual scene undergoes repositioning across the retinal surface (Castet & Masson, 2000; Gibson, 1954; MacKay, 1973). To maintain visual stability during such ocular motion, the brain is able to distinguish between self-initiated eye movements and external changes to maintain visual stability. The absence of this ability would result in individuals constantly experiencing a persistent blur with each eye movement (Gibson, 1954; Kowler, 2011; Matin, 1974; Wurtz, 2008).

The necessity of being able to distinguish between self and external stimuli is a vital mechanism (Bell, 2001). Self-generated stimuli are sensory experiences or information that originate internally from an individual's own actions or bodily processes. On the other hand, externally generated stimuli are sensory experiences coming from the environment, not created by the individual's actions but instead perceived from the world around them (Ody et al., 2023; Wolpert, 1997; Wolpert et al., 1998; Wolpert & Flanagan, 2001). Electric fish, renowned for their unique electroreceptive abilities, provide an example of such use of distinguishing between self- and externally stimuli types in the animal kingdom (Bell, 2001). As this species is equipped with electric organs to produce their own electric currents, the animals have the ability to discern their self-generated electric fields from external variations through the impedance of proximate objects. In order to prevent the self-produced electric current from interfering with its ability to perceive the environment, the self-generated current is systematically filtered out from the output of the electrosensory cells of the fish (Bullock, 1982). Attenuating self-produced signals for unrestrained perception of externally generated signals enables the electric fish to navigate and locate prey underwater (Bastian, 1999).

1.2 Sensory attenuation

Effects of self-generated signals being perceived as attenuated compared to externally-generated signals, have been observed in diverse domains of human perception. The phenomenon has been termed sensory attenuation (SA). SA is characterized by the reduced subjective perception of self-generated sensory stimuli compared to externally generated ones (Blakemore et al., 1998, 1999; Press et al., 2020; Schröger et al., 2015). The effect has been shown in different modalities, such as in the auditory (Repp, 1987; Sato, 2008; Weiss et al., 2011b, 2011a), tactile (Bays et al., 2005; Blakemore et al., 1998; Shergill et al., 2003) as well as visual domain (Cardoso-Leite et al., 2010; Storch & Zimmermann, 2022, but see Schwarz et al., 2018). For instance, for SA in the context of tactile perception, active interaction with an object or surface prompts the brain to generate predictions concerning the anticipated sensory feedback (Blakemore et al., 1998; Hesse et al., 2010). This prediction is based on previous experiences with similar objects or surfaces (Wolpert & Flanagan, 2001). Consequently, when prediction and perception match, the incoming perceptive signals are attenuated (Blakemore et al., 2000, 2002). A sensory discrepancy occurs in case of a mismatch between the predicted and the actual motor output. The brain adapts to such a sensory discrepancy by adjusting its expectations for future movements. For example, when a pianist plays a piano with slightly different key sensitivity than their usual instrument, a sensory discrepancy arises as his fingers anticipate a different resistance level. Gradually, in response to this sensory incongruity, the pianist adapts by fine-tuning the force applied to the keys.

The process of SA is vital for maintaining a stable sense of self and body ownership. It ensures that our own actions are perceived as less intrusive and helps us filter out irrelevant sensory information (Kilteni & Ehrsson, 2017a). SA is believed to be a natural mechanism of the brain that minimizes incoming sensory information, protecting us from being overwhelmed (Blakemore et al., 2000). From an evolutionary perspective, SA is meaningful as it allows animals, including humans, to ignore sensory events arising from

their own behavior and to accurately detect actions of potential threats, such as predators (Crapse & Sommer, 2008).

1.3 Distinguishing sensory attenuation from other phenomena

SA is frequently mentioned alongside other phenomena, such as intentional binding or the sense of agency. Intentional binding refers to the subjective compression of time between a voluntary action and its consequent sensory outcome (Haggard et al., 2002; Haggard & Clark, 2003). For instance, when pressing a button, an immediately perceived sound is noted despite a slight physical temporal delay between the action and the auditory feedback. Both SA and intentional binding involve the subjective perception of a relationship between actions and sensory outcomes but focus on different aspects. SA pertains to the perceived intensity or salience of the sensory outcome, whereas intentional binding relates to the perceived temporal relationship between the action and the sensory consequence (Blakemore et al., 1999; Haggard et al., 2002; Haggard & Clark, 2003). In terms of testing the two phenomena experimentally, SA is often studied through tasks where participants generate a sensory stimulus and compare its perceived intensity to a stimulus that is externally generated (e.g., Bays et al., 2008; Klaffehn et al., 2019; Weiss et al., 2011). On the other hand, intentional binding is typically investigated using tasks where participants perform an action (e.g., pressing a button) and subsequently estimate the perceived temporal interval between the action and the sensory outcome (Suzuki et al., 2019; Wolpe et al., 2013). The underlying processes for both phenomena are not proven with certainty. SA is believed to arise due to predictive processing mechanisms that suppress the neural response to self-generated sensory stimuli (see also Chapter 1.5). Intentional binding, on the other hand, is thought to be influenced by the brain's mechanisms for linking actions and their consequences in the subjective experience of time. It involves the integration of motor signals and sensory feedback (Haggard et al., 2002). To conclude, while both SA and intentional binding

involve the subjective perception of the relationship between actions and sensory outcomes, they emphasize different aspects.

Another related phenomenon to SA is the sense of agency, which refers to our subjective experience of being the initiator or controller of our own actions and their outcomes. It is the feeling that we are the ones responsible for producing a specific action and that resulting consequences are directly linked to our intentional behavior (Gallagher, 2000). The sense of agency encompasses the awareness and attribution of our own actions as being self-generated and under our volitional control (David et al., 2008; Haggard, 2017). SA is primarily concerned with the perceived intensity or attenuation of the sensory stimulus itself. It relates to the perception of the sensory consequences of our actions and does not directly involve judgments about one's own agency or self-recognition. In contrast, the sense of agency involves the very same processes of self-recognition and the attribution of one's own actions and their consequences to oneself. The effect is not bound to one modality but rather associated with a network of brain regions, including the prefrontal cortex, premotor areas, and the temporoparietal junction, which are involved in action monitoring, self-awareness, and agency attribution (Haggard & Chambon, 2012; Nahab et al., 2011). In summary, SA is about how our brain processes and distinguishes self-generated sensory information, while the sense of agency is about our subjective feeling of being in control of our actions and their outcomes. Notably, the presence of the sense of agency effect is pivotal for SA, as the brain's ability to distinguish between self-generated and externally produced events is a requirement for the occurrence of the phenomena of SA.

1.4 Theoretical models for sensory attenuation

1.4.1 Forward Model

SA is commonly explained by the so-called Forward Model (Jordan & Rumelhart, 1992; Kawato, 1999; Miall & Wolpert, 1996). The Forward Model suggests that humans are able to predict how the execution of motor commands affects the movement patterns of

the limbs and to anticipate the duration and end of movements. Motor commands are signals the brain generates to control the movement of muscles and limbs. These commands specify the desired action or trajectory of the movement (Kawato, 1999).

According to the Forward Model theory, the brain generates a so-called efference copy of motor commands and uses it to predict the sensory consequences of movements (Hughes et al., 2013a; Wolpert et al., 1995; Wolpert, 1997). An efference copy is a copy of a motor command that is sent from the brain to the body to produce a movement (Von Holst, 1954). The efference copy is generated in the brain and then sent to the brain's sensory processing areas before the movement is executed so that the sensory consequences of the movement can be predicted. This prediction allows the brain to compare the expected sensory consequences of the movement with the actual sensory feedback received after the movement is executed (Angel, 1976; Bays et al., 2008; Desmurget & Grafton, 2000; Kawato, 1999; Wolpert et al., 1998). By comparing the predicted and actual sensory feedback, the brain can determine whether the movement was successful or not and adjust future movements accordingly (Miall & Wolpert, 1996). The efference copy is thought to play an important role in motor control, perception, and cognition. It allows the brain to predict and control movements in real time and may also be involved in higher-level cognitive functions such as self-awareness and consciousness (Kilteni et al., 2020).

Miall & Wolpert (1996) illustrated a detailed representation of the Forward Model, see Figure 1. They sketched out the model using the example of processing an incoming motor command. In general, predicted sensory consequences resulting from the motor command are referred to as reafference. Rafference represents an internal estimate of the expected sensory feedback that would arise from executing the planned movement.

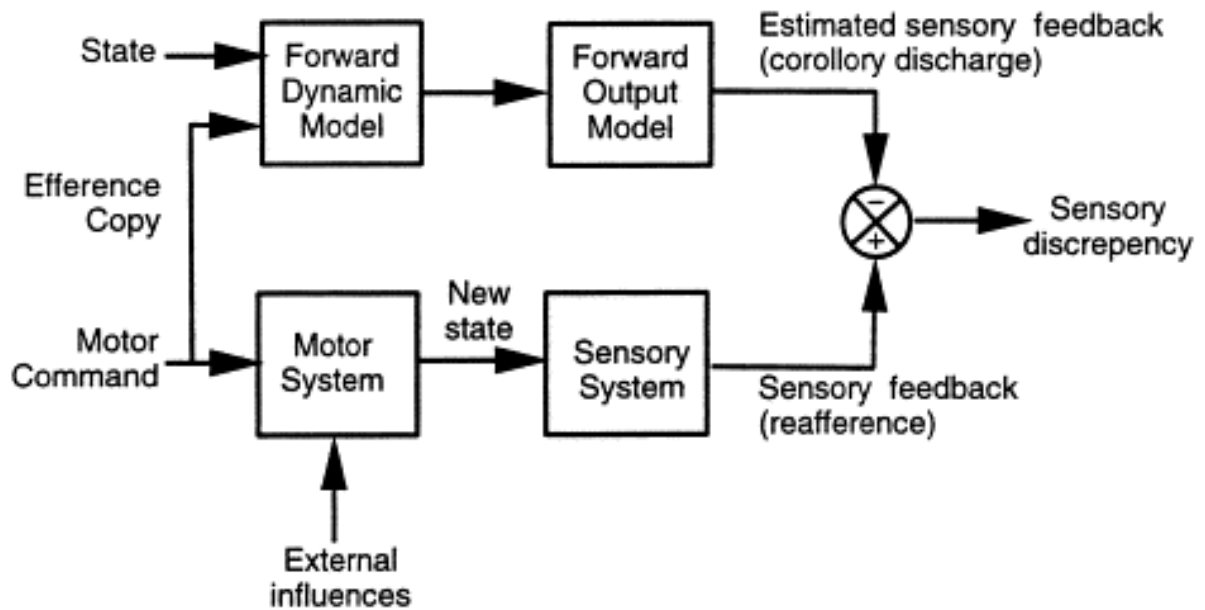


Figure 1. Representation of the Forward Model from Miall & Wolpert (1996).

In the model, by using an efference copy, the forward dynamic model and the forward output model allow the brain to anticipate and predict sensory consequences of voluntary movements. The forward dynamic model is a neural mechanism within the central nervous system (CNS). It predicts and simulates the expected sensory consequences of motor commands before they are executed. For instance, when wanting to raise a limb, the forward dynamic model will use the efference copy of the motor command (the predicted movement signal) and simulate how the limb's muscles and joints will respond to the command. In a second step, the forward output model takes the motor commands as input and directly produces an output prediction of the resulting sensory feedback. The forward output model is part of the process that generates the reafference.

The sensory discrepancy is the difference between the corollary discharge (from the upper row of Figure 1) and the actual reafferent inputs (from the bottom row of Figure 1). It represents the mismatch between the expected sensory feedback and the real sensory feedback during movement execution. Deviations between predicted and actual observed events are also called prediction error (Blakemore et al., 2000; Lindner et al.,

2005). A prediction error can be either positive or negative. A positive prediction error indicates that the model overestimated the actual outcome (e.g., in the case of tactile movements, the intensity of touch), while a negative prediction error suggests an underestimation (Welnarz et al., 2021). The differences between prediction and actual outcome are crucial information that help the CNS to refine its motor control and adapt its predictions for future movements. By minimizing the discrepancy through learning and model adjustments, the Forward Model can improve its predictive accuracy and adapt to changes in the environment or the body (Miall & Wolpert, 1996).

The Forward Model has been used as an explanatory approach in various studies (Miall & Wolpert, 1996; Wolpert et al., 1995). Blakemore et al. (1999) introduced an experiment in which subjects either experienced a self-produced tactile stimulation on their right palm or a stimulation applied externally by a custom-made robotic device. In the external condition, subjects had to move the robotic device's arm, causing a second apparatus to present a tactile stimulus on their right hand. The movement of both hands, as well as the experience of the stimulus on the right hand, did not change throughout the conditions. Only the spatial and temporal predictability between action and consequences was manipulated. Without the subjects' knowledge, delays of 100, 200, and 300 ms were introduced between the movement of the left hand and the resulting movement of the robotic hand. Regarding ticklishness and intensity, the self-produced tactile stimulus was rated as less intense than externally produced tactile stimulation. With increasing delays between tactile stimulation and sensation, the rating of ticklishness increased significantly. A presented temporal or spatial distance between the tactile stimulus and the motor command reduced the attenuation of self-touching and made self-generated stimuli feel more ticklish to subjects. A relationship between the duration of the time interval or the distance between the action and the tactile stimulus and the magnitude of attenuation has been demonstrated. This suggests that internal models generate a temporal prediction of the sensory consequence.

In summary, the Forward Model enables us to generate predictions of the sensory consequences of motor commands (reafference) through a forward dynamic model and compare them with actual sensory feedback during movement execution. This comparison allows the CNS to refine its predictions and enhance motor control for more accurate and efficient movements (Miall & Wolpert, 1996). Forward Models play an essential role in motor learning, as future motor commands are facilitated and more predictable by an internal representation of the movement pattern (Shadmehr et al., 2010).

Although the Forward Model is a well-established approach in the research field of SA, recent studies criticize the model for its complexity, lack of precision, neural implementation as well as its role in cognition (see Desmurget & Grafton, 2000; Dogge, Custers, et al., 2019; Yon et al., 2018). Despite its complexity, the Forward Model may not be precise enough to account for all motor control and perception aspects. Dogge, Custers et al. (2019) criticize the Forward Model theory by suggesting that it may not be able to fully explain the phenomenon of perceptual reafference, which refers to the way that sensory feedback from our own movements can affect our perception of the external world. The authors argue that the brain is only interested in predicting and controlling the sensory consequences of movements, compared to examining how those consequences are perceived. They suggest that the brain may need to take into account how sensory feedback is integrated with prior expectations and attentional factors to produce our subjective experience of the external world. A major criticism point is the currently neglected difference between body- and environment-related action-outcomes (see also Pfister, 2019). The difference between these two action outcomes lies in the type of sensory stimuli involved. Body-related action-outcomes refer to the attenuation of sensory feedback directly associated with one's own body movements, while environment-related action-outcomes involve the attenuation of sensory consequences resulting from self-generated actions impacting the surrounding environment (Dogge,

Custers et al., 2019). Examples of environment-related action outcomes include visual stimuli or tones resulting from button presses, whereas body-related signals include self-generated tones or touch (Bays et al., 2005; Shergill et al., 2003). The differentiation between both types is frequently overlooked, leading to a common association of Forward Models predicting both signals. Dogge, Custers et al. (2019) question the applicability of the Forward Model to these events, especially in terms of environmental-related action outcomes. The authors instead suggest introducing a hybrid prediction model, depending on the action outcome involved in the process. They believe that general predictive mechanisms are more likely to be used in the absence of a previously learned association between sensory events and action. Overall, their criticism suggests that the Forward Model theory may need to be expanded or modified to fully account for the complex interactions between motor control, sensory feedback, and perception.

Recent literature findings such as Press et al. (2020) or Yon et al. (2018, 2021) found amplified instead of weakened sensory consequences. Representations of visual brain areas changed towards expected action outcomes, making an explanation of domain-general ideas more plausible (Yon et al., 2018). The authors hypothesize that increased importance of prediction errors or sensory gating may lead to such attenuating effects. It is worth emphasizing that expectations bias our actions towards perceiving expected outcomes (Yon et al., 2021).

Finally, there is still some debate over the neural implementation of the Forward Model theory. While many studies have provided evidence for the existence of efference copies in various areas of the brain, it is still unclear how these copies are generated and how they are integrated with sensory feedback to produce motor control and perception. In this context, Voss et al. (2008) were able to show that an active movement retroactively attenuates the perception of previously presented stimuli. Subjects prepared the movement of their right finger even before the visual stimulus was presented. Thus, planning an action could be responsible for SA. In a second study by Voss et al. (2006), transcranial magnetic stimulation (TMS) was applied to the premotor cortex to delay a

planned movement and related motor cortex output. The movement was not yet executed by the subjects but only planned. Nevertheless, SA was evident at the time of movement planning. Such effects are challenging to explain solely through the currently prevailing Forward Model, as the motor command causes an efference copy to emerge. The model is the most frequently approach for explaining SA; however, there are also several other alternatives that will be introduced in the following.

1.4.2 Comparator model and predictive coding framework

Simpler alternatives to the Forward Model exist, such as the comparator model (Frith, 1987; Frith & Done, 1989), the corollary discharge theory (Sperry, 1950; Wolpert & Ghahramani, 2000), and the predictive coding framework (Clark, 2013; Friston, 2008). The comparator model states that sensory impressions are compared and evaluated against previous experiences and their consequences (Feinberg, 1978; Frith, 1987; Frith & Done, 1989). While the comparator model provides a general framework for understanding sensorimotor processing, it does not account for all aspects of SA, such as the cancellation of tactile sensory input (Roussel et al., 2013).

A different approach is the predictive coding framework, which suggests that prior information is constantly used by our brain to generate predictions about upcoming events (Clark, 2013; Friston, 2003, 2005; Huang & Rao, 2011; Rao & Ballard, 1999). This generative model consists of a set of neural representations that encode predictions about the causes of sensory inputs at different levels of abstraction. At the lowest level, sensory representations encode raw sensory data, such as visual or auditory inputs. At higher levels, more abstract representations encode predictions about the causes of the sensory inputs (Clark, 2016; Rao & Ballard, 1999). The brain's goal, within this framework, is to minimize prediction errors. Prediction errors occur when there is a mismatch between the predicted and actual sensory inputs. When prediction errors are high, it suggests that the current predictions about the causes of sensory inputs are incorrect, and the brain needs to update its predictions (Friston, 2008). For such an

update, the brain employs a process called predictive coding. Predictive coding involves two types of signals: prediction signals, which flow from higher-level representations to lower-level representations, and prediction error signals, which flow from lower-level representations to higher-level representations (Grill-Spector & Malach, 2004). The prediction signals convey top-down predictions about the causes of sensory inputs. In contrast, the prediction error signals convey bottom-up information about the mismatch between the predictions and the actual sensory inputs. By constantly updating its predictions based on prediction errors, the brain can refine its model of the world and generate more accurate perceptions (Friston, 2010). In conclusion, the predictability of processes plays a central role within the framework. Being able to predict a stimulus influences the strength of SA, but it is not a necessary factor for the phenomenon to occur. What is more crucial is the involvement of self-generation of a motor command as such movements serve as a reliable predictor for drawing conclusions (Kiepe et al., 2021). The occurrence of SA is thus less dependent on predictability and more on self-initiated movement. As a result, the current predictive processing framework may need to be reevaluated to include the role of self-generated action in SA (Kiepe et al., 2021).

1.4.3 Other models

Alternative theories propose that motor suppression or inhibition mechanisms may also be involved in SA (Aliu et al., 2009). For instance, research has shown that SA is more pronounced when the motor command for a self-generated movement is actively inhibited, as opposed to when it is executed without inhibition. This suggests that suppressing motor activity may be a means by which the brain diminishes the salience of self-generated sensory input (H. Brown et al., 2013; Han et al., 2021). The proposed models are thus more broadly formulated, but they also provide limited specific statements.

All the presented models are used to explain the phenomenon of SA. However, as described above, they encounter limitations. The models may be too specific or unspecific to provide comprehensive explanations for all underlying action processes. At present, the Forward Model remains the most prevalent and frequently employed theory for explaining SA effects. Still, having multiple models depending on the modality and examined action is beneficial to offer a more comprehensive understanding. To improve and refine the models in the future, it is essential to fully understand the phenomenon of SA. This includes gaining a better understanding of the underlying brain processes involved.

1.5 Neuronal components of sensory attenuation

Neuronal aspects of SA have been primarily assessed within the auditory domain using electroencephalography (EEG) recordings. An EEG is a neuroimaging technique used to measure event-related potentials (ERPs) in the field of neuroscience and cognitive psychology (Blackwood & Muir, 1990). ERPs are electrical brain responses extracted from the EEG that are time-locked to specific sensory or cognitive events, such as the presentation of a stimulus or the execution of a motor action (Picton et al., 2000). Within the context of emerging EEG analysis techniques, ERPs can offer valuable information about how the brain's response to self-generated stimuli differs from externally generated stimuli. The approach provides a direct and objective measure of the brain's processing of incoming sensory signals and contributes to our understanding of sensory perception and motor control (Martikainen et al., 2004; Näätänen & Picton, 1987). Currently, the neuronal basis of SA remains an active area of research, with multiple theories and findings shedding light on this phenomenon (Lange, 2013). EEG studies have measured attenuated N1 responses for self-generated stimuli, predominantly in the auditory domain (Baess et al., 2011; Martikainen et al., 2004; Schafer & Marcus, 1973; Timm et al., 2014). The auditory N1 component is an ERP that occurs in the brain in

response to auditory stimuli (Davis et al., 1939; Näätänen & Picton, 1987). It is a negative deflection in the electrical brain activity recorded using EEG or magnetoencephalography (MEG). The N1 component typically appears around 100 ms after the onset of an auditory stimulus, although its latency and characteristics can vary depending on factors such as stimulus properties and experimental conditions. The auditory N1 component is believed to reflect the early stages of auditory sensory processing and the detection of acoustic features of the stimuli. It is often considered to be associated with the initial encoding and categorization of auditory information (Ford et al., 2007; Mifsud & Whitford, 2017).

The P2 component is a positive peak in the ERP that follows the N1 component. It typically occurs around 200 to 300 ms after stimulus presentation (Mifsud & Whitford, 2017). Attenuation of the P2 component was also observed for SA (Bolt & Loehr, 2021; Egan et al., 2023; Klaffehn et al., 2019). However, its role is less well-understood compared to the N1 component (Crowley & Colrain, 2004; Klaffehn et al., 2019). Korka et al. (2022) propose that these two components rely on distinct underlying processes, suggesting findings in one component cannot be generalized. Consequently, the subsequent paragraph primarily centers on the N1 component.

Attention and prediction affect the processing of auditory stimuli and how these factors contribute to the modulation of the auditory N1 component. To address these inconsistencies, Lange et al. (2013) propose a model that associates the diverse findings on the auditory N1 with the opposing effects of attention and prediction. According to the model, attention enhances the processing of attended sounds and leads to an increased N1 amplitude, whereas prediction decreases the processing demands and results in a decreased N1 amplitude. The authors suggest that these attention and prediction mechanisms interact in shaping the processing of auditory stimuli.

N1 attenuation has been observed not only when comparing self-generated sounds to externally generated ones but also when comparing sounds resulting from the actions of

another person to externally generated sounds (Ghio et al., 2018). Other studies, such as Weller et al. (2017), found no differences between predictable self-generated and externally generated auditory signals for the N-1 component.

EEG and MEG studies have revealed that SA is associated with decreased neural activity in sensory regions like the auditory and the anterior cingulate cortex, alongside increased activity in areas involved in prediction and error detection, such as the supplementary motor area (SMA) (Blakemore et al., 2000; Jo et al., 2019). The cerebellum has been found to play an important role in the implementation of motor learning, coordination, and control (Paulin, 1993; Wolpert et al., 1998). It is also implicated in SA by generating predictions of the expected sensory outcomes of motor commands, such as encoding temporal prediction errors related to SA (Blakemore et al., 2001). Increasing activity in the anterior and posterior cerebellum has been recorded when manipulating temporal intervals between self-generated stimuli and sensory feedback (Arikan et al., 2019). Longer intervals between self-generated stimuli and sensory feedback might lead to more neural activity, resulting in less SA. This suggests that the level of neural activity in relevant brain regions may contribute to the modulation of SA. The cerebellum is thought to contribute to the Forward Model by comparing predicted sensory feedback with actual sensory feedback, thus influencing the perception of self-generated stimuli. This is supported by the findings of Knolle et al. (2013a) who demonstrated that cerebellar patients do not exhibit an N100-suppression effect in response to self-initiated sounds when these are presented together with externally-produced sounds.

Moreover, motor-related predictions involve the activation of the motor cortex and associated brain areas (Svoboda & Li, 2018). The motor cortex, which includes the primary motor cortex and SMA, plays a crucial role in generating voluntary movements (Ikeda et al., 1992). It is involved in generating motor commands and the associated predictions of the sensory consequences of those movements (Friston et al., 2009). The motor cortex activity contributes to the top-down modulation of sensory processing during self-generated actions, leading to SA (Voss et al., 2006).

Historically, EEG findings and behavioral outcomes have been examined independently. Ody et al. (2023) represent pioneers in simultaneously addressing both EEG and behavioral assessments. In current studies, the behavioral aspect is often overlooked, with results simply extrapolated. Consequently, this dissertation seeks to provide an extension of SA effects within the realm of behavior.

To summarize, it is important to note that SA is a complex process that likely engages a network of brain regions, including those involved in motor control, prediction generation, attention, and sensory processing. The specific contributions of these brain regions may vary depending on the sensory modality and experimental context, and the precise underlying neuronal processes still remain unclear (Horváth, 2015; Hughes et al., 2013a, 2013b).

In this regard, the application of TMS can be useful. TMS is a non-invasive neurostimulation technique used to modulate brain activity. With the help of a coil placed on the scalp, cortical neurons in a targeted area can be excited or inhibited, depending on stimulation (Chen et al., 1997; Macerollo et al., 2015; Massimini et al., 2005). In the context of SA, the amplitude of motor-evoked potentials (MEPs), which are induced by TMS and measured in peripheral muscles, show an increase during action preparation and a decrease when actions are voluntarily inhibited (Tran et al., 2021). The motor system's output undergoes prediction-driven attenuation. Effects manifest even when participants refrain from executing any actions themselves (Tran et al., 2021). Voss et al. (2006) were able to demonstrate that SA during voluntary movements originates from an upstream efferent signal of the primary motor cortex. Thus, for the underlying mechanisms of SA, the application of TMS holds great promise. However, Ross et al. (2022) emphasize the challenge of accurately matching the sensory experience of active TMS with sham TMS. They propose to use a combination of diverse sensory suppression techniques to optimize the TMS signal. Studying effects of SA in the brain can thus present a challenge, but maintaining the constancy of external influencing factors on the

effect can prove to be equally demanding. Such influencing factors will be described in the following.

1.6 Factors influencing sensory attenuation

Various studies showed that the effects of SA can be influenced by different aspects such as temporal prediction or temporal control (Harrison et al., 2021; Schafer & Marcus, 1973; Weiskrantz et al., 1971), motor and non-motor identity prediction (Hughes et al., 2013) as well as the feeling of authorship (Desantis et al., 2012; Timm et al., 2016). It has been discussed that SA only occurs due to the absence of one of these factors, especially due to temporal control and prediction. The influence of these two factors will be examined in more detail below.

Earlier studies have suggested that auditory SA is reduced when stimuli are not temporal predictable (Schafer & Marcus, 1973; Sowman et al., 2012). This means that, e.g., temporally predictable tones lead to a stronger SA than unpredictable tones. In the tactile domain, Weiskrantz et al. (1971) demonstrated that participants reported a stronger ticklish sensation when they were tickled by a custom-built machine compared to when they held the machine's lever passively with predictable timing. This implies that the temporal predictability of the tickling stimulus alone can diminish the subjective perception.

Temporal control is the ability to regulate and manipulate the timing of actions, events, or processes. It involves the capacity to coordinate actions and make adjustments based on temporal constraints, goals, or expectations (Aschersleben, 2002; Killeen, 1975). Temporal control is essential in executing precise and coordinated movements. It involves the ability to regulate the timing and sequencing of occurring stimuli as well as allowing individuals to perform tasks with accuracy and efficiency (Hughes et al., 2013b). Weiss et al. (2011b) found stronger attenuation for sounds when self-generated stimuli

were produced in response to an external command compared to completely self-timed stimuli. However, in this study, both temporal control and motor identity prediction were manipulated (Hughes et al., 2013b). A contradictory outcome was described in an EEG study, wherein diminishing temporal control over a stimulus resulted in a decrease in N1 amplitude (Harrison et al., 2021). Apart from these studies, few experiments explicitly examining the direct impact of temporal control on SA have been conducted. Thus, further research explicitly investigating the impact of temporal control on SA is warranted to advance knowledge in this area.

Temporal control is closely linked to the ability to make accurate predictions about the timing of future events, which is known as temporal prediction. Temporal prediction involves estimating when an event will occur based on past experiences, patterns, or temporal cues (Schafer & Marcus, 1973; Sowman et al., 2012; Weiskrantz et al., 1971). Regarding sensory events, temporal prediction is described as the competence to predict the exact moment of event occurrence (Hughes et al., 2013b). Earlier studies showed that SA did not occur, when temporal predictability was not present (Schafer & Marcus, 1973; Sowman et al., 2012). On the other hand, recent studies found SA for self-generated stimuli independent of temporal predictability (Bäß et al., 2008; Lubinus et al., 2022). Klaffehn et al. (2019) controlled temporal predictability with the help of a visual cue. Participants were asked to trigger tones by pressing a button or passively listening to tones generated by the computer. Results showed that SA still occurred (attenuation of auditory N1 component) even when controlling for temporal predictability. In an EEG study, Horváth et al. (2012) suggested that the contiguity between action stimuli is sufficient to find attenuation effects.

In conclusion, the question of how temporal control and temporal prediction impact SA has not yet been definitively resolved. Harrison et al. (2021) suggested that both of these factors are not sufficient to explain the overserved effects of SA, but when controlling for both, SA increased. Temporal control seems to be even more important for attenuation,

as studies showed that attenuation occurred for temporally controlled stimuli, although temporal prediction was absent (Bäb et al., 2008). However, there are limited studies that investigate temporal control as an influencing factor on SA. Temporal control is automatically present in self-generated movements as such movements are predictable and can be planned in detail. A prediction of the occurrence of a stimulus is directly matched with the participant's action. This allows one to focus attention on the stimulus just before onset. Consequently, if the manner in which attention is allocated varies between the self-generated stimulus and the externally generated stimulus, it may not effectively compensate for the potential distinctions caused by temporal attention. To prevent the intertwined effects, Hughes et al. (2013b) suggest comparing conditions in which a sensory event is consistently prompted by an action, but the specific connection between the action and the sensory event is deliberately manipulated.

Another explanation is that both temporal control and temporal prediction may be enough to cause a decrease in sensory intensity. Combining both factors would amplify this effect. This idea aligns with previous research that demonstrated a diminished decrease in intensity when accounting for temporal prediction (Hughes et al., 2013a; Schafer & Marcus, 1973; Weiskrantz et al., 1971).

Lastly, it is important to mention that effects may also differ depending on the modality tested. The studies described in this paragraph relate predominantly to visual and auditory SA. A growing body of evidence suggests that the mechanisms underlying SA may exhibit modality-specific characteristics. These findings imply that distinct neural processes and cognitive mechanisms may contribute to SA in different sensory domains (Hughes et al., 2013a; Kaiser & Schütz-Bosbach, 2018). In the tactile domain, several studies (e.g., Bays et al., 2005, 2006; Blakemore et al., 1998) showed effects of SA despite the predictability of stimulation following their actions. One explanation is that SA is observed when the body-part involved in the action is in motion (Chapman et al., 1987). SA in the tactile modality is predominantly referred to as self-touch. SA for self-touch has to be distinguished from other attenuation effects as it is an evolutionary,

meaningful, occurring phenomenon that is universal across individuals (Kiltner & Ehrsson, 2017b). In contrast, for external events, such as pressing a button and attenuating the resulting sound, the connections between events have to be learned through experiences (Bays et al., 2005; Hughes et al., 2013a). As a result, SA for self-touch is based on characteristics not applying to all areas of attenuation, such as the factors of spatial and temporal specificity, which are described in the upcoming chapters.

1.7 Spatial specificity of sensory attenuation for self-touch – Objectives for Study 1

Earlier studies showed that SA for self-touch is spatially specific (Bays et al., 2006; Hughes et al., 2013b; Knoetsch & Zimmermann, 2021). Spatial specificity in this context pertains to the precision with which the phenomenon is confined to a particular spatial region or location within a domain-specific system (Knoetsch & Zimmermann, 2021). For example, when the right index finger makes contact with the left arm, tactile feedback simultaneously occurs on both involved limbs. The spatial extent of tactile sensations is consistent to the extent that actual sensory and motor experiences proportionately match. This phenomenon is commonly referred to as the *touchant-touché* situation (Cataldo et al., 2021; Merleau-Ponty, 1976; Schütz-Bosbach et al., 2009).

The effect of spatial specificity for self-touch has been shown in current literature (Bays et al., 2005; Hughes et al., 2013b; Knoetsch & Zimmermann, 2021). However, the exact underlying mechanisms in the brain and circumstances under which such specificity occurs are still unclear. Is the visual feedback of seeing the contact of touch sufficient to confirm self-touch or is there a specialized mechanism that calculates the spatial distance between the touching and the touched limb? What role does proprioceptive information play during SA for self-touch? In Study 1, we aimed to address these research questions by clarifying the distinct contributions of vision and proprioception in the context of self-touch. A virtual reality (VR) design was utilized to deliberately modulate visual and

proprioceptive cues during self-touch movements to discern the factors conducive to spatial specificity.

1.8 Temporal specificity of sensory attenuation for self-touch – Objectives for Study 2

A similar tuning phenomenon is also likely in the characteristic of temporal specificity of self-touch. In previous studies, attenuation effects were no longer observed in experimental conditions from Bays et al. (2005) or Blakemore et al. (1999) due to a slight delay of 100 ms between the touching and touched body-part. From an evolutionary perspective, such pronounced specificity in this domain appears meaningful, allowing for rapid responses to the changing environment. Self-touch is no longer attributed to self-generation but is perceived as externally generated when presented with a delay to the touched hand. In contrast, Kilteni et al. (2019) were able to show temporal recalibration for self-touch. In their study (Kilteni et al., 2019), they demonstrated a novel approach of the brain learning to adapt to such a temporal delay between touching and touched body-part with SA still being present. Participants unlearned the expectation of self-touch occurring temporally synchronized with a self-generated movement and instead learned to anticipate a temporally delayed sensory consequence. Following an adaptation phase during which a 100 ms delay between the touching and touched fingers was presented, participants showed attenuation effects in delayed conditions. Kilteni et al. (2019) identified this effect for a 100 ms delay. The question remains whether SA subsequently diminishes after this 100 ms interval or is prolonged. Secondly, it is questionable whether the learning effect is confined solely to an interval of 100 ms. This was one of the main objectives in Study 2. We sought to find out whether SA persists even after a prolonged delay, such as 400 ms or no longer shows. Furthermore, we examined whether the predictability of the interval had an impact on the strength of the effect.

Consequently, the presentation of temporal intervals was either organized blocked or randomized.

To summarize, in the first two studies, we aimed to examine the temporal and spatial specificity for SA during self-touch. As numerous concurrent processes are set in motion during the emergence of SA, we assume that attention is directed towards the tactile domain in these moments. Meanwhile, processes in other domains are expected to be downregulated. This hypothesis was the focal point of investigation in our third study.

1.9 Motor-induced attention shifts – Objectives for Study 3

Auditory SA is highly prevalent in current literature. As described in Chapter 1.5, the majority of studies that have investigated EEG effects pertain to the auditory modality (Bäb et al., 2008; Egan et al., 2023; Klaffehn et al., 2019; Lange, 2011). While an evolutionary rationale exists, the plethora of processes responsible for auditory SA remain a subject of ongoing research. Our first two studies demonstrated the simultaneous occurrence of spatial and temporal specificity during self-touch. This comparison process can be, depending on the movement, attention consuming. Especially in goal-directed movements, such as button-presses, the tactile attention is likely to increase towards the movement goal as the touching hand expects tactile feedback. Similar effects have been shown for pointing movements (Baldauf et al., 2006). It appears necessary to reduce the capacity for other domains during this period. We propose to find such decrease in the auditory modality, due to its functional connectivity to the tactile modality (Butler et al., 2012; Iguchi et al., 2007; Nordmark et al., 2012). We aimed to test this approach in our third study using a VR design. We hypothesized that during goal-directed movements SA in the auditory domain occurs due to tactile attention shifts to the moving hand.

By investigating the spatial and temporal specificity of SA in different modalities, we can deepen our understanding of how the brain integrates self-generated actions and sensory inputs to construct our conscious perception of the world. Understanding these mechanisms is crucial not only for elucidating fundamental principles of sensory processing but also for unraveling the complex interplay between self-generated actions and sensory perception. Such knowledge holds promise for advancing basic scientific understanding as well as for potential applications in clinical settings, VR, and human-computer interaction.

2 Overview of Studies

In the dissertation, three studies dealing with SA in the auditory and tactile domains are described. All experiments were in accordance with the Declaration of Helsinki and were approved by the local ethics committee of the Faculty of Mathematics and Natural Sciences of Heinrich Heine University, Düsseldorf (identification number: 757184). Participants were recruited at the University of Düsseldorf or via social networks. Subjects voluntarily participated in the studies and gave their written informed consent. The following sections include conceptual summaries of the three studies. Full details are provided in the original research articles and manuscripts, which can be found in Appendix B.

2.1 Study 1: The spatial tuning of sensory attenuation for self-induced touch: body-part identity or body-part position?

The first study has been submitted for publication in *Scientific Reports*.

2.1.1 Introduction

The human perceptual system comprises multiple sensory modalities that combine to provide a coherent representation of the external world and our own bodies (Holmes & Spence, 2005). Such processes within the body also play a pivotal role in the emergence of SA. According to the Forward Model, the process of attenuation only occurs when the estimated sensory feedback, originating from the efference copy, and the actual sensory feedback (afference copy) match (Jordan & Rumelhart, 1992; Miall & Wolpert, 1996; Wolpert et al., 1998). If the two copies are not identical, a mismatch between what the brain anticipates occurs, which is called sensory discrepancy (Miall & Wolpert, 1996). Sensory discrepancy can occur due to various factors. For instance, Bays et al. (2005) were able to demonstrate that SA does not emerge when the temporal congruence between self-initiated touch and the resultant sensory feedback is artificially delayed.

Furthermore, the spatial position of touch plays a crucial role. Knoetsch and Zimmermann (2021) demonstrated that SA is spatially selective by occurring exclusively in relation to the touched finger. The effect was not transferred to other regions, for instance, the ring finger. In their study, however, the hand to be touched was not visible throughout the experiments. Consequently, participants relied on their proprioceptive signals. Opposing effects were observed in studies where self-touch was visually perceivable. For instance, within the context of the Rubber-Hand-Illusion, it has been shown that visual feedback to touch one's own hand is sufficient to induce SA (Botvinick & Cohen, 1998; Costantini & Haggard, 2007; Tsakiris & Haggard, 2005). These contradictory findings suggest that the availability of visual information can influence the incorporation of proprioceptive signals. The question arises: What is more relevant in terms of visual and spatial information for the occurrence of SA for self-touch: the body-part identity or the body position?

We conducted three major studies in a virtual environment to address this research question. In the virtual environment, we were able to manipulate the visual position of participants' left arm, as both arms were depicted with 3D models. We aimed to estimate first whether we could find classical effects of SA between a passive no-movement condition and an active pointing task within the virtual setting. In the active pointing task, participants were asked to point towards the middle of their left arm, where a vibromotor was attached. In the exact moment of touching the virtual target and thus the physical vibromotor, a vibration occurred. A second vibration occurred 750 ms later, and participants were asked to decide which vibration felt stronger.

In a second experiment, we altered the observable visual location of the touch in VR relative to where the physical tactile stimulation occurred. As participants were instructed to direct their pointing movements towards a visual target, we were able to manipulate the spatial alignment of this visual target with the subject's physical arm. In one scenario, the VR environment featured the visual target coinciding with the position of the

vibromotor attached to the participants' physical arm. Conversely, in another scenario, the virtual target aligned with an object specifically designed to replicate the tactile sensation experienced when the arm was touched. We found no differences between scenarios as the visual signal did not alter. Thus, in the third experiment, we varied the visibility of the touched arm to investigate our initial research question. We aimed to examine the respective influences of the visual and proprioceptive signals in predicting the location of self-induced tactile sensations on the arm.

2.1.2 Methods and Results

We conducted one baseline measurement with $N = 59$ participants. For the other three experiments, we included $N = 50$ participants for Experiment 1, $N = 70$ participants for Experiment 2, and $N = 57$ participants for the last experiment.

Experiments were conducted in a VR environment. Participants were seated in front of a table in the virtual world, resembling the physical lab environment. Participants' arms were placed on the table. The left arm was fixated with two plastic loops, whereas the right arm was movable.

In the baseline measurement, participants only saw the virtual table in front of them. A blue bar was positioned slightly to the left of their field of view on the virtual table. The subjects' task was to estimate whether this virtual bar would be stationed to the left or right of their physical arm. Six bar positions were introduced with a 1, 2, or 3 cm displacement to the left or right of the physical arm position. We fitted mean correct responses with psychometric functions and calculated PSE and Just Noticeable Difference (JND) values for the experiment. The mean JND value above participants of $M = 1.17$ shows that the discrimination ability to locate the physical arm was around one cm. We conclude that we find an uncertainty in the estimation of one's physical arm position when immersed in the virtual environment.

In Experiment 1, the general setting remained the same. In the virtual environment, participants saw the table in front of them but also their virtual right and left arms. They were asked to perform two different conditions: an active pointing condition and a passive non-movement condition. Conditions were presented randomly. In the active pointing condition, their task was to touch a virtual target presented on their left virtual arm. The virtual arm position matched with their physical arm position. When touching the virtual target, a vibration occurred on the participants' left arm, mimicking the touch. A second vibration occurred 750 ms later at the same position, and participants were asked which vibration felt stronger by the help of a foot pedal.

Conversely, no pointing movement had to be performed in the passive non-movement condition. Participants were immersed in the virtual environment. Trials started automatically with two vibrations being presented on their left physical arm. Subjects' task was to indicate which vibration felt stronger by entering the response with a foot pedal. One second after the response, the next trial started automatically.

A dependent samples t-test between the active and passive conditions revealed attenuation effects in the active pointing condition. We found SA for self-touch.

In Experiment 2, the general setting and task remained the same. In the active pointing condition, participants were asked to point towards a virtual target and decide which of the two occurring vibrations felt stronger. However, in Experiment 2, the virtual target was randomly positioned on three physical target points: the physical arm, a fake object 4 cm left of the physical arm, or a fake object 6 cm left of the physical arm. All three physical target positions were equipped with a vibromotor, so the sensation on the touching left finger was comparable. In the virtual environment, participants visually always touched their virtual arm. After every trial, we shifted the virtual arm position, so we introduced a mismatch between the physical and virtual arm positions. For example, when participants aimed to touch the dot presented on the virtual arm, the physical target position was randomly positioned either on the physical arm or on one of the two fake objects. After touching the virtual target, a vibration occurred, followed by a second vibration 750 ms

later. Subjects were asked to decide which vibration felt stronger.

In the passive condition, participants saw the virtual arm on one of the three target positions introduced in the active pointing condition (0 cm, 4 cm, 6 cm). As described in Experiment 1 they were asked to passively judge the intensity between two vibrations. We found a significant effect between the active pointing and the passive non-movement condition. This indicates that SA was present in the pointing condition. The differences between positions showed no significant effects. We conclude that the visual signal suffices to compare the spatial touch location, so no further comparison with the proprioceptive signal is evoked.

In Experiment 3, we introduced the same tasks and target manipulations described in Experiment 2. However, in Experiment 3, the virtual left arm was not visible throughout both conditions. In the active pointing condition, participants were asked to point towards three different target positions around the physical left arm (0 cm, 4 cm, 6 cm). The target was randomly positioned on one of these three positions, but only the visual target dot was shown. The left virtual hand was invisible. The differences between Experiments 2 and 3 can be seen in Figure 2.

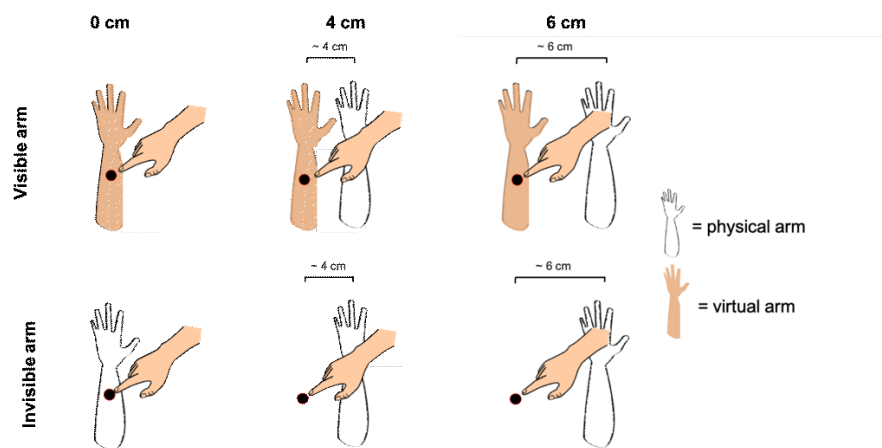


Figure 2. Differences between active pointing conditions in Experiments 2 and 3.

After touching the visual target, a vibration occurred through the vibromotor on participants' left arm, followed by a reference vibration 750 ms later. Participants were asked to judge which of the two vibrations felt stronger.

We found a difference in attenuation between the three arm positions (0 cm, 4 cm, 6 cm). Attenuation for the furthest target (6 cm) was strongest, whereas attenuation for the physical target position (0 cm) was lowest. This indicated that attenuation increased the further outside the target was shifted.

2.1.3 Discussion

In earlier studies, it has been demonstrated that SA is spatially selective and only occurs if the feedback of touch matches with where the finger actually touched the hand (Knoetsch & Zimmermann, 2021). Miall & Wolpert (1996) suggest that for SA to occur, a continuous comparison between the expected feedback and the feedback actually received from the motor command is needed. As previous studies showed, the process takes into account both spatial and temporal components (Bays & Wolpert, 2007; Kilteni & Ehrsson, 2017a; Knoetsch & Zimmermann, 2021). The more closely these two components match, the stronger the attenuation becomes. Our primary goal in the study was to determine whether the comparison between predicted and actual sensory outcomes of self-touch relies more strongly on proprioceptive or visual signals.

To validate our VR setup, we showed the classical effect of SA in the first experiment. We demonstrated that an active pointing movement towards a virtual target with the right hand was perceived as weaker than a passive touch signal. The virtual target position matched with the physical and virtual left arm. Participants touched their left arm and received matching visual and proprioceptive feedback. The attenuation of this self-generated touch compared to a passive non-movement condition is consistent with previous findings (Bays et al., 2005, 2006; Blakemore et al., 2000).

In a second experiment, we manipulated the position of the virtual target. The virtual target was presented not only on the physical arm but also at two other positions, shifted

4 and 6 cm left from the physical arm position. In VR, the virtual arm was shifted to the target positions so participants always had the visual impression of touching their own arm. Thus, we were able to introduce a mismatch between the visual and the proprioceptive feedback in conditions where the virtual target was shifted further outward. We found that when a visual representation of the arm is present, the brain relies on this visual estimation of arm position, as sufficient evidence of self-touch is provided. We found SA compared to a passive non-movement condition for all three physical hand positions (0 cm, 4 cm, 6 cm).

In a third experiment, we did not present a visual left arm, but the same target shifts of target position (0 cm, 4 cm, 6 cm). We expected the sensorimotor system to rely solely on proprioceptive signals, the only remaining source of information for determining the touch location. In the active pointing condition of Experiment 3, we observed that SA accounted for the discrepancy between the physical and virtual arms. SA became more pronounced as the mismatch between the pointed virtual target and the physical arm increased. We conclude that SA for self-touch is determined by the comparison of both body-part identity and body-part position. However, the comparison of the body-part is dominant. When vision confirms that the touched part corresponds to the expected body-part, no additional processing of further information, such as of the proprioceptive system, appears to be required. This process is efficient for typical real-life perception as the alignment between visual input and the corresponding proprioceptive signal is predominantly identical. In cases where visual input is unavailable, proprioception provides an estimate of the body-part's position, which is then compared to the efference copy signal representing the body-part's position. SA occurs when these two signals spatially align.

2.2 Study 2: Temporal adaptation of sensory attenuation for self-touch

The second study has been published as an open-access article in the Journal of Experimental Brain Research and can be found via the following link:

<https://link.springer.com/article/10.1007/s00221-023-06688-5>

2.2.1 Introduction

Temporal recalibration refers to a phenomenon in which our perception of the temporal relationship between sensory events can be adjusted or recalibrated based on our recent experience (Harrington & Haaland, 1999; Van Der Burg et al., 2015). Specifically, it involves the adaptation or realignment of our internal temporal processing mechanisms to match the temporal discrepancies between different sensory signals. By recalibrating the timing of sensory events, the brain can improve the synchronization and integration of sensory signals, leading to a more accurate and coherent perception of the world around us (Fujisaki et al., 2004; Vroomen et al., 2004).

Kilteni et al. (2019) investigated whether the effect of temporal recalibration also occurs for SA for self-touch. They demonstrated that the brain can unlearn the expectation of self-touch occurring temporally synchronized with a self-generated movement and instead learn to anticipate a temporally delayed sensory consequence of 100 ms (Kilteni et al., 2019). Continuing with this approach, in our first experiment, one of the main objectives was to find out whether SA persists even after a prolonged delay. We sought to find out whether the effect can be trained to occur longer than 100 ms, such as 400 ms, or if it just disappears after an exposure to a 100 ms delay. Thus, we asked whether the learning of temporal shifts in SA can be significantly delayed, which, to the best of our knowledge, has not been addressed in previous literature. Secondly, we wanted to examine if the blocked vs. randomized presentation of test delays leads to different effects as the predictability in a randomized design is decreased. We varied this factor in two experiments. By comparing the magnitudes of SA for randomly occurring test delays (no-

movement baseline, 0 ms, 100 ms, and 400 ms), we expected that the effects of temporal recalibration would no longer be present.

In our first experiment, we randomized the presentation of the different test delays (no-movement baseline, a delay of 0 ms, a delay of 100 ms, and a delay of 400 ms). We did not observe any effects related to temporal recalibration. We could not verify the hypothesis of possible learning processes for delaying SA effects for self-touch. To further investigate this lack of effects, we conducted a similar setup in experiment 2 but without manipulating the order of test delays. Each test delay was presented in a fixed block of 20 test trials. Despite these efforts, we still did not find any significant effects of exposure delay on the delay between action and sensation. Thus, experiment 3 was designed as a conceptual replication of the study conducted by Kilteni et al. (2019).

2.2.2 Methods and Results

We conducted three experiments within the study. In Experiment 1 and 3, we included data of 36 participants. In Experiment 2, we included 40 participants. We calculated sample sizes on the basis of effect sizes from the study of Kilteni et al. (2019).

In all three experiments, participants were asked to place their left index finger under a custom-built lever mounted on an apparatus placed in front of them. Their right index finger was resting above a force sensor. When participants pressed the force sensor with their right index finger, a corresponding lever touch was felt on the left index finger. The lever rotated with a delay of either 100 ms before the right index finger press (no-movement), with no delay (0 ms), 100 ms delay or 400 ms delay. We observed that the test delays were modulated in line with the exposure delay, consistent with a temporal recalibration of SA. During exposure trials, participants heard an auditory go signal to press the force sensor with their right index finger. After pressing, the lever rotated with either no delay (0 ms) or a 100 ms delay after pressing the force sensor, depending on the condition conducted. During test trials, participants heard an auditory signal and

2 Overview of Studies

when they pressed the force sensor, the lever rotated two times. The first lever rotation (test tap) occurred either 100 ms before (no-movement baseline), with (0 ms), 100 ms after, or 400 ms after the test tap, depending on the test delay. The second lever rotation (comparison tap) always occurred 1000 ms after the start of the first rotation and varied in its intensity with a subjectively perceived intensity of 1.7 to 2.3 N (Experiment 1 and 2) or 1.4 to 2.6 N (Experiment 3). Subjectively perceived N values were determined previously in a short pilot testing. The temporal outline of the different test delays can be seen in Figure 3.

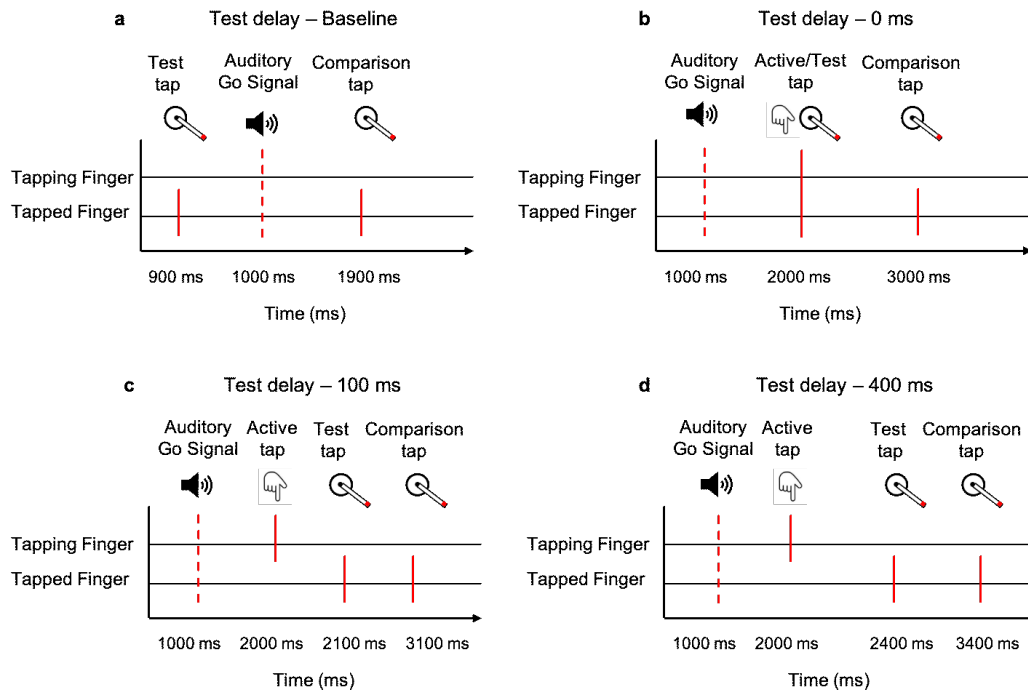


Figure 3. Temporal outline of the three different test delays in Experiments 1 and 2.

After feeling the comparison tap in the test trials, participants were asked to decide whether the first or second tap felt stronger with the help of a foot pedal.

Experiment 1

Experiment 1 was divided into two sessions and started with 500 exposure trials with a delay of either 0 ms or 100 ms between force sensor press and lever touch. Afterwards, the four test delays (baseline, 0 ms, 100 ms, and 400 ms) were presented in test blocks in a randomized order. One test block for each test delay consisted of five exposure trials (with either 0 or 100 ms delay) and one test trial (baseline, 0 ms, 100 ms, and 400 ms). We conducted 20 test blocks for each test delay, adding to 980 trials in total per session. Each participant underwent two sessions, with the initial session randomly starting with either a 0 ms delay or a 100 ms delay in exposure trials. A staircase procedure known as the Best PEST method was used to determine the perceived equality between test and comparison tap (Pentland, 1980). We observed SA for all test delays, but there was no effect of the exposure delay. In order to rule out the potential influence of the random presentation of the different test delays, we conducted a second experiment. In this follow-up, we implemented a blocked design for the presentation of test delays.

Experiment 2

The overall methodological details and task remained similar in Experiment 2 compared to Experiment 1. Participants were asked to press the force sensor with their right index finger after hearing an auditory go signal. In Experiment 2, we introduced a systematic alteration to the sequence of the four test delays, presenting them in a consistent order of 20 test trials per block compared to a randomized presentation in Experiment 1. The order of these blocks was randomized between participants. Again, a session started with 500 exposure trials, which either introduced a delay of 0 ms or 100 ms. Each test delay (baseline, 0 ms, 100 ms, 400 ms) was presented in one test block, where each of the 20 test trials was alternated with five exposure trials. In test trials, a test and a comparison tap were delivered to participants' left index fingers after pressing the force sensor with the right hand. Participants were asked to indicate which tap was stronger with the help of a foot pedal. We found similar results as in Experiment 1. Again, no effect for the

exposure delay was observed, but SA was present for all test delays. As we were not able to find temporal recalibration in the first two experiments, Experiment 3 was a conceptual replication of the study of Kilteni et al. (2019) to find the effects presented in their study.

Experiment 3

Experiment 3 was, with minor adjustments, a replication study of Kilteni et al. (2019) (for adjustments see Appendix B). Every participant had to undergo four sessions during the experiment. The overall task and setting remained similar. Again, we introduced an exposure delay of either 0 ms or 100 ms. For test delays, only delays of 0 ms and 100 ms were examined. Every delay was tested separately; the order was randomized between participants. We chose a broader range for the subjectively perceived magnitudes in Experiment 3 (1.4 – 2.6 N in 7 equidistant steps). Every magnitude was presented ten times during one session. We also changed the duration of tactile stimulation during exposure and test trials from 300 ms in Experiments 1 and 2 to 100 ms in Experiment 3. As participants had to undergo 70 test trials alternated with five exposure trials and started with 505 exposure trials, 925 trials were conducted per session.

In this experiment, we used psychometric functions to determine the perceived equality between the test and comparison stimulus. We observed SA between a test delay of 0 ms and 100 ms. The effect was closely aligned with exposure delays. We did not find an unlearning effect of SA at 0 ms when being exposed to a 100 ms delay during exposure.

2.2.3 Discussion

In this study, our primary objective was to explore two key questions. Firstly, we aimed to investigate the influence of prolonged delays on temporal recalibration of self-touch. Secondly, in Experiments 1 and 2, we aimed to determine whether the random or blocked presentation of test delays impacts the strength of temporal recalibration. To examine these questions, during experiments, participants were instructed to touch their left index finger with their right index finger. With the help of a custom-built device, we

introduced a test delay of either 0 ms, 100 ms, or 400 ms between the right index finger's action of touch and the resulting sensation on the left finger. These test delays were presented in both randomized (Experiment 1) and blocked orders (Experiment 2).

In the first two experiments, we did not observe the traditional effects of SA occurring between a test delay of 0 and 100 ms. Since attenuation was absent, further examination of the temporal recalibration effect was impossible, and we could not assess whether the effect might extend to longer time intervals. As we were not able to find attenuation effects in Experiments 1 and 2, in Experiment 3, we conducted a conceptual replication of Kilteni et al. (2019) to examine the effects of recalibration and attenuation. We observed a significant interaction effect between exposure and test delay. This shows that test delays were influenced by exposure delays, providing evidence for a temporal recalibration of SA. A shift in the temporal alignment of SA to the introduced delay of 100 ms was observed. However, we were not able to show unlearning of attenuation in the corresponding test delay of 0 ms, as found in Kilteni et al. (2019).

The contradictory effects observed between our three experiments could be attributed to several factors, including methodological and analytical differences between Experiment 1 and 2 compared to Experiment 3. Specifically, we varied the analysis method from Best PEST to psychometric curves and included minor methodological changes as described above. Secondly, in comparison to Kilteni et al. (2019), our methods slightly deviated. We did not employ the physical intensity as a reference for magnitude and were unable to retrospectively re-bin delays based on the measured force of the test tap applied to the left index finger (for further differences, refer to Appendix B). However, Bays et al. (2006) were able to demonstrate that a varying intensity of touch does not influence the occurrence of SA. If methodological modifications account for the disparities between studies and experiments, the effect of learning and unlearning SA is relatively small and only observable under specific conditions. We conclude that SA for self-touch appears to be more specific than initially presumed.

2.3 Study 3: Tactile motor attention induces sensory attenuation for sounds

The third study has been published as an open-access article in the Journal of Consciousness and Cognition and can be found via the following link:

<https://www.sciencedirect.com/science/article/pii/S1053810022001180>

2.3.1 Introduction

Providing prior notice through, e.g., a button press that a specific sound is about to follow reduces the sensory cortical response to that sound. This effect of SA for sounds occurs when the generation of a tone is perceived as self-generated compared to externally generated (Weiss et al., 2011a; Weiss & Schütz-Bosbach, 2012). The reduction in sensory cortical response can be observed for both the N1 (McCarthy & Donchin, 1976) and subsequent P2 (Egan et al., 2023; Knolle et al., 2013b) components. When individuals press a button, their brain generates predictions regarding the anticipated sensory outcomes based on past experiences and learned associations. These predictions are then compared to the actual sensory feedback received from the button press. If the predicted and actual feedback align, the brain diminishes the perceptual impact of the sensations generated by the individual's own actions, leading to SA. When a series of pure tones were presented to participants regardless of their button presses, a reduction of N1 suppression was still observed (Horváth et al., 2012). The associated learning from previous experiences was sufficient for attenuation.

SA in the auditory domain, occurring after a button press, is an interesting phenomenon to examine. During such goal-directed, closed-loop movement, the important factor for ending the movement action is the ensuing tactile feedback when pressing the button. We hypothesize that during the movement, attention should shift to the moving hand and

especially to the fingers that are expecting tactile feedback from the button press. To examine this effect, we divided the movement of pressing a button into the three movement phases of starting, moving, and pressing. We anticipated the enhancement of tactile attention towards the end of the movement because the sensorimotor system should await the tactile sensation with highest priority. We were able to find enhancement in the tactile modality in our first experiment. Next, we wondered if this enhancement of attention in the tactile modality might lead to a reduction of attention in other areas, such as the auditory domain. To test this approach, we manipulated the occurrence of tactile feedback when conducting a button press in a virtual environment.

2.3.2 Methods and Results

We conducted three experiments. A post-hoc conducted power analysis on the basis of Fraser and Fiehler (2018) revealed a necessary sample size of $N = 27$ for Experiment 1 and $N = 23$ for Experiment 2. The sample size for Experiment 3 was based on Gillmeister and Eimer (2007). In the first experiment, we tested $N = 29$ participants (including one author) and $N = 29$ different subjects for a Baseline condition. In the second experiment, $N = 25$ participants took part, and in the third experiment, we included $N = 20$ participants.

During the experiments, participants were seated in front of a table in a quiet environment with a VR headset on. Participants were asked to perform a goal-directed hand movement to press a button presented in a VR environment. A virtual hand model was shown in VR that moved synchronously with the real hand. We captured the hand movement of participants with a Leap Motion sensor attached to the VR goggles. A mini vibrotactile motor, controlled by an Arduino Nano, was attached to the participants' right and left index fingers. As a result, tactile feedback could be delivered to the index finger of the moving hand during the movement.

Experiment 1

Trials in Experiment 1 started with a *Ready* message positioned on the left side of the virtual field of view. After a duration of 500 ms, the *Ready* message was substituted with a *Set* message, which remained on the screen for 500 ms. The participant's objective was to press the button precisely at the designated *Go* time, specifically 500 ms, following the onset of the *Set* message. Trials were divided into the three phases based on the timing of tactile stimulations in relation to the go-signal (Start: before the go-signal, Move: simultaneously with or after the go-signal, Press: precisely when the button was pressed). A tactile stimulation varying in its intensity was delivered to the mini vibrotactile motor attached to the participant's right index finger during one of three movements times (Start, Move, and Press) of the hand movement. The timing of the vibrotactile stimulus presentation was randomized across trials, meaning that the vibration could occur during the start, move, or press phase. An outline of the hand movement is shown in Figure 4.

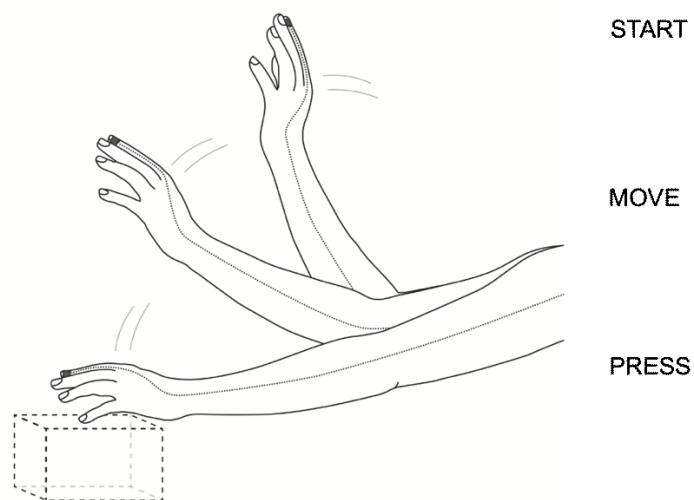


Figure 4. Outline of the phases during button press movement.

Throughout each trial, the vibration applied to the index finger of the right hand remained constant at 50% of the maximum vibration intensity (5 Volt). Following the button press, a comparison vibration was delivered to the index finger of the left hand after a delay of

700 ms. The intensity of the comparison vibration varied randomly between trials, ranging from 20% to 40% and 60% to 80% of the maximum intensity (in 6 equal steps).

We fitted data for each subject for each movement phase with psychometric functions. We found a significant difference between the Start and Press movement phases (one-way repeated measures ANOVA). This indicates that tactile sensitivity during the movement intensified towards the movement goal.

Experiment 2

In Experiment 2, we hypothesized that the increased tactile sensitivity towards the end of the movement observed in Experiment 1 would result in SA for auditory stimuli.

Two conditions were randomly presented to subjects. Either participants felt a tactile stimulation on their right index finger during the button-press movement (tactile), or no tactile feedback (no-tactile) was presented. In both conditions, a probe tone was presented randomly either during the start or press phase of the button-pressing movement (50 % of the maximum intensity), followed by a reference tone 700 ms after the button press (changing between 20% - 40% and 60% - 80%). Since the occurrence of the tone appears self-generated only during a button press movement, it was hypothesized that effects of SA for auditory stimuli can be found in the press phase compared to the start phase. We found SA for sounds only when tactile feedback was provided during the press phase. Attenuation was absent when no tactile feedback was provided.

Experiment 3

To show that SA for sounds in Experiment 2 occurred due to the interaction of button press, tactile feedback and occurring sound, we conducted a passive baseline measurement in Experiment 3. Participants were asked to distinguish tones without

performing the button press movement in VR. First, a reference tone was presented with 50% of the maximum intensity, followed by a comparison tone 700 ms later (changing between 20% - 40% and 60% - 80%). We tested two groups: Participants either experienced a tactile vibration on their left index finger coupled with the reference tone, or no vibration was delivered. We found no attenuation in both groups. We conclude that SA for sounds was not present as it relies on the self-generated button press movement and the simultaneously occurring feedback.

2.3.3 Discussion

Tactile enhancement towards the end of the goal-directed button press movement was observed in the pressing finger. We found the highest tactile sensitivity in the hand during the exact moment of button pressing. We reasoned that an attentional shift towards the pressing finger during the movement could be an explanation for this enhancement. Tactile sensitivity in this specific region increased throughout the movement. This is in line with research from other fields. For example, for eye movements, at the time of saccade onset, attention is bound to the target position (Deubel & Schneider, 1996).

The effect we observed is distinct from tactile gating. Tactile gating refers to the selective modulation or filtering of tactile sensory information, which leads to a reduction of perceiving tactile information during movement (Chapman et al., 1987; Rushton et al., 1981). This phenomenon is observed in various contexts, such as during tasks that require selective attention to specific tactile stimuli or before/during arm movements (Buckingham et al., 2010; Fraser & Fiehler, 2018; Voss et al., 2008; Voudouris & Fiehler, 2017). Usually, the effect is tested by stimulating the elbow or arm with a short vibration. Participants underestimate the intensity of the perceived stimuli during motion. Voudouris and Fiehler (2021) discovered a reduction in sensory gating during the maximum speed of hand movement, followed by an increase towards the end of the

movement. These findings appear to be in contrast with our own results. However, a crucial aspect of our study was that the only stimulus participants received during movement were the probe vibrations of tactile feedback. In the other studies showing tactile gating effects (such as (Juravle et al., 2010, 2017; Voudouris & Fiehler, 2017) tactile feedback was concurrently presented with feedback received from the movement itself (e.g. touching or grasping an object). In our experiment, we were able to fully control for such confound, as we introduced a VR design in which no other sources of tactile feedback were available.

A second notable distinction from previous studies on gating is the goal-directed nature of our movements. Whereas many gating studies do not involve goal-directed actions (e.g. Buckingham et al., 2010; Rushton et al., 1981) we examined the special movement of a button press. When we press a button, the tactile sensation that occurs when the finger touches the button serves as a signal to cease further movement. We postulate that during these goal-directed hand movements, tactile sensitivity is enhanced precisely at the anticipated time when the hand is expected to make contact with the desired object.

The increased attention of the tactile domain leads to reduced attentional resources in other areas, such as the auditory system. We were able to show that the effect of auditory SA only occurred when tactile feedback was provided during movement, and thus, the attentional processes were focused on the tactile domain. Earlier research has documented simultaneous activation of both the somatosensory and auditory cortex (Convento et al., 2018; Iguchi et al., 2007; Nordmark et al., 2012), and the impact of attention on these dual cortical systems was described (Gescheider et al., 1975). We suggest that during the exact moment of button pressing, attention shifts to the tactile modality and thus reducing perception in the auditory modality leading to SA for sound.

3 Discussion

This dissertation aimed to investigate the spatial and temporal specificity of SA in the tactile and auditory modalities. Three empirical studies were conducted. The subsequent discussion provides a comprehensive summary and classification of the research context for the conducted studies.

3.1 Dominance of Body-part Identity over Body-part Position

In Study 1 (The spatial tuning of sensory attenuation for self-induced touch: body-part identity or body-part position?), we aimed to identify the role of body-part identity and body-part position in self-touch movements. We asked whether the spatial distance between the touching and the touched finger is determined in a comparison process or if the mere visual confirmation of observing self-touch suffices to trigger SA for self-touch. To investigate this research question, participants were asked to touch targets presented either on or around their left arm with a pointing movement of the right index finger. We used a VR setting in which virtual arms represented the subject's physical arms. The virtual left arm could be positioned to either coincide precisely with the physical arm's location or be spatially displaced relative to it. Secondly, we varied the presence of visual signals so the left arm was either visually visible or invisible. In Study 1, we showed that as long as the occurrence of touch between the touching and touched arm is visually confirmed, no additional processing is necessary for the occurrence of tactile SA. The actual spatial discrepancy between the touching and the touched body-part is ignored when visual feedback of touching the goal-location is provided. In relation to our research question, we can conclude that a visual observation of self-touch is adequate to initiate SA for self-touch. Such dominance of body-part identity has been shown previously with the Rubber-Hand-Illusion (Botvinick & Cohen, 1998; Costantini & Haggard, 2007; IJsselstein et al., 2006; Tsakiris & Haggard, 2005). In the Rubber-Hand-Illusion, a participant's hand is masked while a rubber hand is placed in front of them. The physical

hand and rubber hand are then simultaneously stroked with a brush. When the sensory input is perceived on the physical hand but seen visually on the rubber hand, the subject may begin to feel a sense of ownership or association with the rubber hand. This results in a drift in their proprioceptive perception. The rubber hand is perceived as a body-part, despite the subjects' cognitive awareness that it is not one's physical hand (Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005). Kilteni & Ehrsson (2017a) found that the mere observation of a rubber hand touching the left hand resulted in SA, indicating that the perceived ownership of the model hand as part of one's own body led to this effect. Attenuation for physical self-touch was reduced when experiencing the rubber hand as belonging to the own body. Participants felt like the real hand was replaced by the rubber hand. Similarly, in Study 1 conducted in this dissertation, it was shown that proprioception pertaining to the body-part being touched was effectively disregarded when visual feedback confirmed the contact of body-parts. The virtual setup allowed us to differentiate proprioceptive from visual information. A dissociation of these signals is uncommonly encountered in real-life situations. Hence, to work efficiently, the brain abstains from initiating an additional proprioceptive comparison during self-touch movements as the visual information suffices.

With the possibility to completely dissolve visual information during the touching movement in VR, the role of proprioception in the absence of vision was further explored. Previous studies found a spatial tuning effect for SA for self-touch (Bays et al., 2005; Hughes et al., 2013b; Knoetsch & Zimmermann, 2021), indicating that the touched position and the touching limb have to be spatially matched. Spatial tuning means that SA for self-touch is more pronounced when the self-generated touch occurs at a specific spatial location, typically near the part of the body that is being touched, as compared to when the touch occurs at a different spatial location (Bays et al., 2005; Knoetsch & Zimmermann, 2021). The touching body-part is located by the efference copy signal the brain generates during internal forward modeling (Kilteni et al., 2020). In Study 1, retrieving the location of the touched body-part became reliant on proprioception in the

absence of vision. A spatial tuning effect for SA during self-touch was demonstrated when visual information was impaired. We found SA for self-touch even when an object further outward of the physical arm was touched during the pointing movement of the right hand. An estimate of the occurring touch was sent via the motor efference copy. When reaching the movement goal, participants received tactile feedback at the touching finger and on the physical arm position. This indicates that the prediction of the efference copy signal was fulfilled, although spatially not aligned as participants pointed further outward. The tuning effect actively processed and compared the spatial information related to the touched body-part. An estimate of the occurring touch was sent via the motor efference copy. This is in line with multisensory conflicts observed in other domains where the brain employs to minimize emerging conflicts by spatially aligning sensory inputs to reduce disparities (Lohmann & Butz, 2017; Salomon et al., 2016). In Study 2, we propose the conflict was dissolved by shifting the proprioceptive arm position further outward. This phenomenon, known as proprioceptive drift, has been frequently observed (Botvinick & Cohen, 1998; Brown et al., 2013; Brown et al., 2003; Tsakiris, 2006).

To conclude, for attenuation of self-touch the role of body-party identity is dominant compared to body-part position. Once a visual signal identifies self-touch between two body-parts, proprioceptive signals are less perceived. This comparison enables efficient processing. In the absence of a visual signal, spatial tuning of proprioceptive information is observed. With these novel finding, we have been able to make a valuable contribution towards gaining a deeper understanding of the phenomenon of SA for self-touch.

3.2 Reduced flexibility in temporal recalibration for self-touch

In our second study (Temporal adaptation of sensory attenuation for self-touch), we investigated the flexibility of the temporal recalibration effect in the tactile domain. Particularly, we were interested in determining whether the temporal recalibration effect

would be limited to the delay introduced during exposure trials or if longer test delays would also be influenced. In a previous study, Kiltani et al. (2019) demonstrated the classical attenuation effect for self-touch in test trials where touching a force sensor with the right index finger was closely followed by a lever touch on the left index finger. Attenuation was not observed when the touch on the left index finger was delayed by 100 ms (Bays et al., 2006; Kiltani et al., 2019). After being exposed to a 100 ms delay between pressing the force sensor and receiving a lever press in 500 trials, participants effectively learned to adapt to the delayed tactile sensation. SA for self-touch was present even when the lever touch occurred 100 ms after the movement. Crucially, Kiltani et al. (2019) demonstrated an unlearning of SA for self-touch effects at the immediate presentation of touch. After the 100 ms exposure, SA was only present at a 100 ms delay, implying that the whole spatial tuning curve shifted. In Study 2, we asked whether this learning and unlearning effect of SA also shows for prolonged delays or if the temporal recalibration effect is timely limited. Additionally, we explored the potential influence of randomized versus blocked presentation of test delays on the strength of temporal recalibration.

In Experiments 1 and 2 of Study 2, attenuation was not found between the delayed conditions of 0 ms and 100 ms, but we found SA for stimuli presented with a test delay of 0 ms compared to a passive baseline. In prolonged delays of over 100 ms, attenuation effects were not found. Due to the absence of effects between the 0 ms and 100 ms conditions, we were not able to examine the effect of temporal recalibration in these experiments. As differences between setups and analysis methods might have been responsible for the absence of effects, in Experiment 3 we aimed to replicate the study of Kiltani et al. (2019). In the third experiment, a modulation of test delays by exposure delays was confirmed. This is in line with the temporal recalibration effect of SA. However, our data do not show that the repeated exposure to a systematic temporal shift

between conducted and received touch is reflected in unlearning of SA. In this regard, we were unable to replicate the results reported by Kiltner et al. (2019).

Differences between our results and Kiltner et al. (2019) might be reflected due to differences in setups (see original of Study 2 in Appendix B). However, we also observed a distinction in our experiments depending on whether a psychometric measurement or a threshold measurement was employed. Both methods are frequently used to determine SA (Bays et al., 2006; Kiltner et al., 2019; Storch & Zimmermann, 2022) as they offer distinct advantages and can be valuable depending on the specific research or measurement objectives. Threshold estimations, such as staircase procedures or maximum likelihood estimation, dynamically adjust the stimulus intensity based on the participant's responses (Levitt, 1971). These methods aim to converge on the participants' threshold quickly and efficiently by adapting the stimulus level based on previous responses (Treutwein, 1995). Threshold estimation can save time by minimizing the number of trials needed to estimate the threshold accurately, such as in Experiments 1 and 2 of Study 2. A psychometric function measurement, in contrast, would have had major disadvantages: Study 2 aimed to assess the non-movement baseline condition in conjunction with three other conditions (0 ms, 100 ms, and 400 ms) within one single experimental session. As we introduced two more conditions compared to Kiltner et al. (2019), signs of fatigue would have played a major role as the experiment would have lasted over four hours in total when applying psychometric functions to all four conditions. A staircase procedure was the more parsimonious method for measuring variable delays in these Experiments. On the other hand, psychometric curves provide a comprehensive representation of the relationship between stimulus intensity and behavioral responses. By measuring responses across a range of stimulus levels, psychometric curves allow for the characterization of sensory thresholds, discrimination abilities, and the shape of the response function (Green & Swets, 1966). The method provides valuable information about an individual's overall sensory performance and can

be used to compare performance across different conditions or populations. By applying psychometric functions in Experiment 3, we were able to gain deeper knowledge of the individual data of subjects at each stimulus level. The curves provided a detailed and comprehensive characterization of sensory performance but also required a larger number of trials to obtain reliable estimates. Experiment 3 lasted over two hours with only two tested delays.

To summarize, threshold estimation methods provide faster results with reduced trial requirements, making them efficient when time is limited or when measuring thresholds in individuals with limited attention or tolerance for prolonged testing sessions (Jones et al., 2015). However, based on the empirical observations from Study 2, the utilization of psychometric functions for SA measurement is advisable, if experimental duration allows. Psychometric functions allow for a more detailed representation of individual data. Study 2 showed that psychometric curves appear to be more accurate when directly compared to data from threshold estimation.

3.3 Temporal and spatial match during sensory comparison process

Another aspect identified in Study 1 and 2 pertains to the comparison process introduced within the Forward Model. This comparison involves the continuous evaluation of the estimated sensory feedback resulting from a motor command with the actual sensory feedback received from executing the motor command (Desmurget & Grafton, 2000; Kawato, 1999; Wolpert et al., 1998). The Forward Model shows that when both estimated sensory feedback and sensory feedback match, the sensory reaction to the motor command is attenuated. In case of a mismatch, SA does not occur (Miall & Wolpert, 1996). Instead, the sensory system notifies of potential discrepancies (Weiskrantz et al., 1971). Within the model, the comparison between sensory feedback

and estimated sensory feedback is mentioned but not further elaborated upon. In Studies 1 and 2, we looked specifically at this comparison process. We were able to demonstrate that two factors are predominantly considered in this process: time and space.

The temporal match of processes involved in the emergence of attenuation effects is critical for SA to occur (Bays et al., 2006). In the case of a sensory event (such as self-touch), the temporal predictability of the occurring feedback is crucial and pronounces the effect of SA (Harrison et al., 2021; Hughes et al., 2013b). However, even if the self-touch movement and the associated tactile feedback do not occur simultaneously, with one of the two components happening at an earlier or later time, Kilteni et al. (2019) showed that SA can still occur. As we have shown in Study 2, this effect is less flexible than previously assumed. However, to this end, research suggests that a spatial tuning curve is responsible for the occurrence of SA. Tactile intensity decreases approximately 300 ms before self-touch and takes around 300 ms to increase again after the occurrence of touch (Bays et al., 2005). We propose that this temporal tuning effect runs within the comparison process of the Forward Model.

Secondly, the spatial alignment between the estimated and actual sensory feedback plays a critical role. In Study 1, we were able to demonstrate that proprioception provides an estimate of the body-part to be touched when the visual signal is absent. The prediction of the contact to be felt on the touched body-part is subsequently compared to the efference copy signal, indicating the position of the touching limb. When both signals align spatially, SA occurs. The spatial comparison is important for SA of self-touch. We propose the incorporation of space and time during the comparison process should be included into a revised model, as depicted in a broad outline in Figure 5.

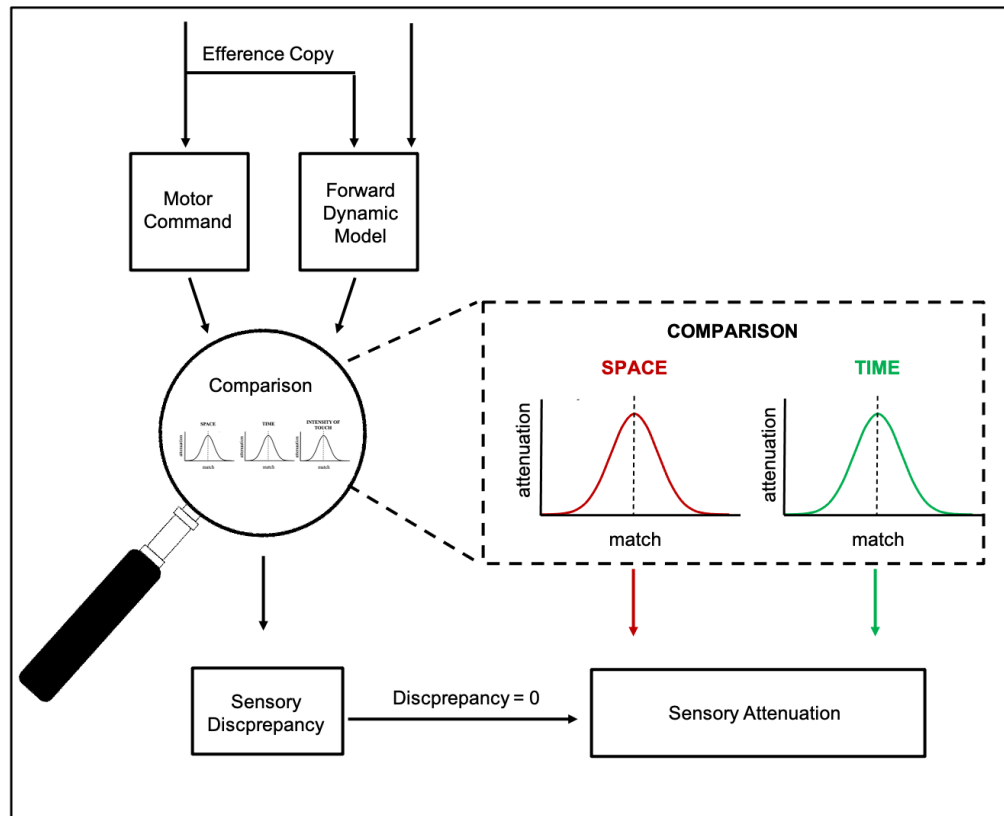


Figure 5. Schematic illustration of a revised model architecture involved in SA of self-touch.

In the figure, we zoom in on the comparison process conducted between estimated and actual sensory feedback. We propose that sensory discrepancy can only be minimized when sensory feedback of the motor command matches approximately in space and time with the estimated feedback from the efference copy.

3.4 Attentional shifts to the tactile modality induce attenuation for sounds

In our third study (Tactile motor attention induces sensory attenuation for sounds), we introduced a new approach to explain SA for sounds generated through closed-loop

movements such as button presses. We designed a VR experiment in which participants were asked to perform a goal-directed movement to press a virtual button which induced a sound. During the button-pressing movement, we found an increase in tactile perception towards the movement goal. In previous research, it has been shown that the detection of tactile stimuli presented to the arm or the hand was decreased during movement (Colino et al., 2017; Colino & Binsted, 2016). This phenomenon has been termed tactile gating or tactile suppression (Chapman et al., 1987; Williams et al., 1998). Juravle et al. (2010) showed such suppression effects in a reach-to-grasp hand movement. In their study, participants were instructed to grasp a designated target object upon the auditory presentation of a *go* signal. Subsequently, when a secondary auditory *go* signal was presented, participants were asked to reach for a second target object positioned in front of them. A significant increase in tactile thresholds during the execution phase of the movement in comparison to the initiation or grasping phases was found. Such tactile gating effects have to be distinguished from the tactile enhancement effect observed in Study 3. Firstly, the latter involved a goal-directed button-pressing movement with significant task relevancy. Manzone et al. (2018) showed that the degree of suppression is task-dependent, with targeted movements displaying a comparatively lower level of suppression. In the context of a button-pressing movement, where tactile feedback plays an indispensable role in terminating the action, task relevancy is maximized. Secondly, in studies such as the one presented from Juravle et al. (2010) or Voudouris and Fiehler (2017), tactile thresholds during the grasp phases were measured intertwined with the actual tactile feedback received from touching the goal object. When the object was grasped, both the tactile stimulus and feedback from touching the object were presented simultaneously. The perceived intensity from the tactile stimulation may have been influenced by the presence of tactile feedback from the object. However, during the movement phases, the latter feedback was not present as the reaching movement was conducted without holding the target object. The presence and absence might have been a major confound for tactile threshold measurement. As Study 3

presented in this dissertation was conducted in a VR setup, no confounding tactile stimulation was present during the movement. We were able to control and evenly present tactile feedback during all movement phases of button-pressing.

With tactile sensitivity being enhanced towards the end of the movement goal, we hypothesized that attentional resources were primarily allocated to the tactile modality during the moment of button-pressing. A shift of attentional resources has been frequently observed in other modalities, e.g., for eye movements. Deubel and Schneider (1996) showed that attention is focused on the target position shortly before the onset of a saccade. A shift of attention is meaningful to predict the sensory outcomes occurring after a movement and to enable movement success. As similar effects have been presented for pointing movements (Baldauf et al., 2006), we hypothesized that at the exact moment of pressing the button in Study 3, attention was shifted to the moving finger to prioritize processing. This is in line with the enhanced tactile sensitivity found in the first experiment. During this attentional shift, other regions should receive comparatively diminished focus as attention is bound to the tactile modality. We propose that such a decrease in sensory processing pertains to the auditory cortex due to its network connectivity with the human somatosensory cortex (Nordmark et al., 2012; Schürmann et al., 2006). The functional connectivity of the two modalities has been shown in various studies (Butler et al., 2012; Iguchi et al., 2007; Nordmark et al., 2012). For example, in a recent TMS study, performance in an auditory frequency discrimination task was impaired when participants' primary somatosensory cortex (S1) was stimulated while they were asked to simultaneously focus their attention on tactile frequency information (Convento et al., 2018). Thus, in Experiment 2, we tested if such an absence of attention in the auditory modality is responsible for SA in the auditory modality.

Recent findings for visual stimuli specified that the absence of a visual target dissolves the focus of attention (Szinte et al., 2019). Concurrently, we propose that the presence of tactile feedback is pivotal for SA in the auditory modality to occur. To investigate this hypothesis, we tested attenuation for sounds either in the presence or absence of tactile

feedback. As expected, SA for sounds was only present when tactile feedback was simultaneously provided during the button press. In the absence of tactile feedback during the button-press movement, we found no attenuation effects. We propose that missing attentional resources in the auditory domain are responsible for the occurrence of auditory SA during goal-directed movements. To show that the movement of button-pressing is responsible for the attentional shift to occur, we included a passive non-movement condition. Participants were asked to passively distinguish auditory signals with tactile stimulation being either present or not. We found no effects between the two conditions, which is in line with studies of Timm et al. (2014), who found SA for sounds only in movement conditions.

Findings from the third study represent a new approach to explain SA for sounds. We presented that attentional shifts to one modality (tactile) can constrain the available processes in another modality (auditory). We conclude that a shift of attentional resources to the pressing finger was responsible for the tactile enhancement observed during button-pressing in Study 3. During the time of attention shifting towards the tactile modality, the missing attentional resources in the auditory domain might be a cause for SA for sounds.

Although we were able to significantly contribute to ongoing research with our conducted studies, the exact processes contributing to spatial and temporal specificity of SA in all domains need to be investigated further. We suggest that the comparison of spatial and temporal information during SA is specialized depending on the available signals in different contexts (see Study 1) and operates with great temporal precision (see Study 2). Furthermore, a shift of attention towards these comparison processes might be responsible for attenuation effects in other modalities (see Study 3). However, precise statements regarding this matter are difficult to derive, as some limitations within the research context have restrictive effects.

3.5 Limitations

A difficulty in SA research is the absence of standardized protocols and methodologies among studies investigating the effect. This results in variations in experimental designs, stimulus parameters, and measurement techniques, making it challenging to compare and reproduce findings (Dogge, Hofman, et al., 2019). In our second study, we encountered difficulties replicating the effects of temporal recalibration found by Kilteni et al. (2019). An influencing factor might be inconsistencies between setups. With our apparatus used, we were not able to validate if forces from the rotating lever were correctly applied to the participant's fingertip. We cannot rule out that minor finger movements caused changes in the physical intensity felt. This would, in consequence, change the levels of psychometric functions. In the study of Kilteni et al. (2019), applied forces were re-binned for the analysis in case they were differently received on subjects' fingertips. Nonetheless, we secured the finger to a fixed position, and Bays et al. (2008) found no differences between the occurrence of SA and the corresponding intensity of touch (for further differences see Appendix B). However, importantly, if these factors were to have such a strong influence on temporal recalibration, it appears that the effect might be smaller and less generalizable than previously assumed. In this case, SA seems to be a highly specific phenomenon. In future investigations, attention should be paid to the modality, stimuli, type of task (including motor or non-motor processes), and the temporal predictability and control with which tasks are administered. Only with reliable control of these factors, comparability between studies can be ensured. It is essential to structure current research in the field of SA more rigorously to clarify and delineate the effects.

Secondly, the phenomenon of SA is highly context-dependent. The magnitude of attenuation can vary depending on various factors, such as the addressed task, experimental conditions, and individual differences. This makes it challenging to establish consistent and generalizable findings across different contexts. It is unlikely that observed attenuation effects from one modality, e.g., the auditory domain, extend fully to

other sensory modalities such as to tactile and visual stimuli (see also Dogge, Custers, et al., 2019). It seems more likely that while the effects are similar, the underlying perceptual characteristics are markedly different. Each sensory modality has its own unique characteristics and neural mechanisms, so the factors contributing to SA may differ across modalities. For example, for self-induced touch, it has been shown that although SA occurs quite reliably, it can differ depending on the area tested and the type of movement (Chapman et al., 1987). Thus, when extrapolating findings from one domain to the other, further research is needed to approve.

Moreover, the experimental tasks used to study SA may influence the perception of sensory stimuli. Factors such as attention, task engagement, and cognitive load can potentially modulate the magnitude of SA. Attention can be divided into endogenous and exogenous areas (Desimone & Duncan, 1995; Pashler, 2016). Endogenous attention refers to the voluntary allocation of attention based on internal goals, expectations, or task instructions (Egeth & Yantis, 1997). It involves a top-down process where attention is consciously directed to specific stimuli or features. When endogenous attention is engaged, it can enhance sensory processing and perception, potentially modulating the magnitude of SA (Coull et al., 2000; Coull & Nobre, 2008). For example, if individuals are instructed to focus their attention on self-generated stimuli, they may exhibit increased awareness and perception of those stimuli, leading to reduced SA. Exogenous attention is driven by external stimuli or events that capture attention automatically. A bottom-up process is initiated where attention is drawn to salient or unexpected stimuli in the environment (Desimone & Duncan, 1995). This means SA can be influenced by the order of sensory information processed. If a surprising externally generated stimulus captures attention, it may interfere with the SA of self-generated stimuli, resulting in reduced or altered SA (Hughes et al., 2013a). Consequently, in some cases, attention may enhance SA by increasing the perceptual contrast between self-generated and externally generated stimuli (Eimer & Driver, 2001; Hughes et al., 2013a; Nguyen et al., 2020). In other cases, attentional processes may disrupt SA by redirecting focus away

from self-generated stimuli or interfering with the predictive processing mechanisms involved in SA.

3.6 Future directions

The presented studies provided valuable insights into spatial and temporal specificity of SA. However, there remain intriguing avenues for future research to expand and refine our understanding of this phenomenon. In the following section, several promising areas for further studies are discussed.

In the first study, we were able to make a significant contribution to the understanding of spatial tuning of SA for self-touch. We observed stronger SA when participants were asked to touch an outward shifted target position perceived as their physical arm position. In the experiment, only three distinct shifted arm positions were present (0 cm vs. 4 cm vs. 6 cm). It would be interesting to examine the spatial extendibility of this shift. At a certain distance, self-touch should feel implausible for participants, potentially leading to a reversal of the effect and a lesser extent of SA being observed. This distance, however, might be subjective. In further studies, the original experiment could be expanded to include additional fake arm positions. Secondly, positions should be tested also to the right side of participants left arm, so further inward. According to a JND of a ± 1.17 in our baseline measurement in Study 1, spatial uncertainty should refer to the outward as well as inward position of participants' left arm.

Further, in the context of this study, it would be interesting to examine a sample of visually impaired participants. One of the conclusions drawn from Study 1 is the presence of an ongoing comparison between visually perceived and proprioceptive sensations. Cappagli et al. (2017) suggest that in visually impaired children and adults, the development and robustness of proprioceptive spatial representations encounter potential delays or even substantial weakening. They attribute this phenomenon to the

absence of visual calibration across the auditory and haptic modalities. This indicates that individuals with impaired vision rely heavily on proprioception while also experiencing difficulties with spatial perception. Consequently, it would be interesting to examine whether we can find the shifted perception of their physical arm as well. This would show an application context of our research in the clinical domain.

For Study 2 (Temporal adaptation of sensory attenuation for self-touch), it would be interesting to vary minor methodological details in the experimental setup. As such, the duration of stimulation, stimulus intensities, and the type of stimulation could be adjusted. If temporal recalibration for SA prevails, the effect seems to be specific and precise to environmental influences. Secondly, it would be interesting to investigate under which specific circumstances the temporal recalibration effect occurs. Initially, testing was supposed to be conducted using a blocked design, wherein a delay is repeatedly presented consecutively. The influence of randomizing delays can only be examined when a stable effect becomes evident in this design. This question remains intriguing for further investigation. To conclude, the flexibility and temporal manifestation of attenuation effects is of interest. Findings would provide a more detailed insight into the temporal flexibility of SA.

A challenge in Study 3 (Tactile motor attention induces sensory attenuation for sounds) was the varying temporal predictability of the auditory signal during the movement in Experiment 2. Participants were asked to conduct a pointing movement to press a virtual button. The corresponding auditory signal occurred randomly with the button-press or at the beginning of the movement. Thus, the stimulus was not fully predictable. To control this factor for further experiments, we introduced a new approach in an upcoming study. The idea is to perform a pointing movement to press a virtual button, which will trigger an auditory event. The virtual button consistently appears in the same position in the VR environment. In the physical world, the position of the physical button to be

pressed varies. If virtual and physical button positions match, participants receive tactile feedback at the pointing finger. Otherwise, no tactile feedback is provided as the physical button position is not matched with the virtual button position. In this way, the auditory signal is temporally aligned with the virtual button press. The varying factor is the occurrence of tactile feedback. In an adaptation phase, the participants will initially learn the association between pressing a button (simultaneously in VR and the physical world) and producing a tone. Subsequently, the trials will be presented in a ratio of 80% with tactile feedback and 20% without tactile feedback (or vice versa). According to the Forward Model an expectation of receiving tactile feedback will be introduced. To replicate Study 3, an attenuation effect should be observable in the condition in which tactile feedback is presented. If attenuation effects are observed in both conditions, a learned association beyond tactile feedback is likely.

Secondly, in regard to Study 3, it would be interesting to explore the transferability of the phenomenon of SA for goal-directed movements to different body-parts. For instance, the tactile sensitivity of soccer players during the movement of a soccer kick is an interesting phenomenon. Like a button press, a kicking movement is goal-directed and executed until receiving tactile feedback (e.g., from hitting the ball). During the execution of this movement sequence, attention may shift away from the auditory modality towards the striking foot. For testing this hypothesis, an experiment conducted in a virtual environment would be a feasible approach. Participants are instructed to kick a virtual ball towards a goal wall. When kicking the virtual ball, participants receive tactile feedback on the corresponding foot and hear an auditory signal that the ball was hit. The auditory and tactile feedback produced when hitting the ball is manipulable. A design similar to that in Study 3 of the dissertation could be introduced. The probability of occurrence of the tactile or auditory feedback could be manipulated. When introducing tactile feedback during the beginning, in the middle and at the end of the kicking movement, we would anticipate a shift of attention towards the tactile modality (the kicking foot). At the time of attention shifting, SA in the auditory modality should show.

Lastly, it would be meaningful to examine our research questions beyond behavioral experimental designs. A detailed investigation of the brain areas involved in the cognitive processing can be conducted with the help of EEG. EEG allows for a more precise mapping of the engagement of various brain areas within SA. As mentioned earlier, the effect of SA is often associated with a reduction in the N1 (Aliu et al., 2009; Baess et al., 2011; Ford et al., 2007; Martikainen et al., 2004) and P2 component (Bolt & Loehr, 2021; Egan et al., 2023; Sowman et al., 2012). It would be interesting to observe whether the findings of SA in our studies hold true for EEG results as well. Specifically, for Study 2, the incorporation of EEG would be valuable since a highly specific finger movement is conducted. The hand movements conducted in the other two studies are more complex and thus only limitable observed in an EEG study.

To summarize, we introduced broader possibilities for addressing future research questions within behavioral and EEG designs. We can deepen our knowledge of SA and its implications for various domains by addressing these future directions.

3.7 Conclusion

In this dissertation, we introduced several new empirical findings on spatial and temporal tuning processes involved in the occurrence of SA for self-touch and sounds. In Study 1, we showed that information about the body-part identity is dominant compared to body-part position during self-touch. When self-touch is visually observed, proprioceptive information is neglected. In the absence of visionary information, SA for self-touch only occurs when the information between touching and touched body-part matches. The available sensory signals are crucial for the emergence of SA. Secondly, we demonstrated that SA is less temporally flexible than initially assumed, as no temporal learning effect for prolonged delays for SA for self-touch was found in Study 2. We state that adopting standardized methodological approaches is essential in SA research, both in the analysis procedure and the experimental design planning to ensure comparability across studies. Thirdly, we were able to show that a shift of attentional processes towards another modality are likely to play a role in the emergence of auditory SA during goal-directed movements (see Study 3). We found a shift of attention towards the tactile modality during button-pressing movements. Only in the presence of tactile feedback these shifts were found and led to the occurrence of SA in the auditory domain. Attention, although related to the phenomenon of attenuation, has been neglected in many studies so far. Based on our findings, we recommend investigating attention as a confounding or triggering factor for SA in future studies.

In summary, this dissertation contributes to understanding the temporal and spatial specificity of SA within the tactile and auditory modalities.

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Appendix A: 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, den 06. November 2023

Name: Clara Fritz

Unterschrift:

Appendix B: Original Research Articles

Original manuscript of Study 1

Fritz, C. *, Bayer, M. *, & Zimmermann, E. (2023). The spatial tuning of sensory attenuation for self-induced touch: body-part identity or body-part position? *Manuscript submitted for publication in Scientific Reports*.

MB and I were the main authors of this article and share the first-person authorship. We both contributed to the development of the paradigm, created the experimental setup and conducted data acquisition. I conducted data analysis and wrote the initial draft of the manuscript. MB designed the virtual reality setup. All authors contributed to writing several drafts of the paper and approved the final version of the manuscript for submission.

Original manuscript of Study 2

Fritz, C., & Zimmermann, E. (2023). Temporal adaptation of sensory attenuation for self-touch. *Experimental Brain Research*, 1-12.

I was the main author of this article. EZ and I developed the study concept. Both authors contributed to the study design. I performed data collection, data analysis, and interpretation under the supervision of EZ. Both authors contributed to writing several drafts of the paper and approved the final version of the manuscript for submission.

Original manuscript of Study 3

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I was the main author of this article. EZ and I developed the study concept. All authors contributed to the study design. MF and I performed testing and data collection. I conducted the data analysis, contributed to the interpretation of the results, wrote the initial draft of the manuscript, and cooperated with the co-authors on the following versions of the manuscript.

Main Manuscript for

The spatial tuning of sensory attenuation for self-induced touch: body-part identity or body-part position?

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Summary

When we touch ourselves, we feel the pressure attenuated compared to someone else touching us. Theories of sensory attenuation involve a prediction process that compares the predicted and the actual sensation. A spatial match between the touched body part and the touching finger is a precondition for sensory attenuation to occur. Here, we ask whether this comparison rests upon body part identity or position. By using a 3D arm model in a virtual reality environment, we dissociated the visual from the proprioceptive arm signal. When a virtual arm was visible, we found that sensory attenuation generalized across different locations. When no virtual arm was visible, we found that sensory attenuation was spatially tuned. We conclude that a simple check of body-part identity suffices to confirm self-touch when the body-part can be seen. In the absence of vision, the spatial position is compared between the touched body-part and the touching finger.

Introduction

When we touch ourselves, we experience the ensuing sensation differently than when someone else touches us¹⁻³. The most famous example is the inability to tickle ourselves. Apart from the absence of ticklishness experiences, we also feel a self-touch as less intense, a phenomenon termed sensory attenuation^{4,5}. Sensory attenuation is considered the classic example of how internal predictions about the sensory consequences of our actions shape our perception^{1,5}. Distinguishing sensations produced by stimuli in the external world from sensations generated by our movements is vital for a successful interaction in our environment. For instance, if we would not be able to predict that stimulation on the retina is produced by our own eye or head movements, we would constantly feel dizzy and incapable of keeping balance. Sensory attenuation for self-touch must be distinguished from sensory attenuation of external events, such as sounds generated by pressing a door-bell⁶. Predicting the tactile sensations of self-touch might be important to avoid the alarming reaction that we experience when small animals crawl across our skin. If the actual consequences of our actions match the predictions, we experience these sensations as less intense¹. However, for sensory attenuation to occur, it is not necessary that the force applied on a body part matches the force perceived⁷. Brain imaging studies found that in somatosensory cortex processing is attenuated for the predicted consequences of our actions⁸⁻¹⁰. In order to provide a clear-cut distinction between externally and internally generated sensations, predictions must be precise. Deviations of the actual sensations from the predictions should be experienced since these might be caused by external events that we should be aware of. Predictions of the sensory consequences of our movements are provided by the so-called Forward Model, which is built up by the efference copy^{11,12}. Once the movement is executed, the brain compares the predicted sensory consequences from the Forward Model with the actual sensory feedback. This comparison allows the brain to detect any sensory discrepancies between the expected and actual outcomes^{13,14}. However, to this end, a fine-tuned process must compare predicted and actual sensations (see Figure 1). Studies reported a fine temporal and spatial tuning of the sensory attenuation effect¹⁵⁻¹⁷. If the coincidence between the time of the touching and the reception of the touched experience was artificially delayed, sensory attenuation was not observed¹⁵. Similarly, the spatial distance between the touching and the touched finger determines the strength of sensory attenuation¹⁷⁻¹⁹. However, the spatial tuning of sensory attenuation must be evaluated carefully. Does a mechanism calculate the spatial distance between the touching and the touched finger or does vision of both hands simply confirm or disconfirm if self-touch took place? The latter process arguably requires less computational resources compared to the former since only a single visual judgement answers the question. Such a visual determination of self-touch does not evaluate the spatial coordinates of the body-parts and therefore cannot be considered as tuning. The former process instead would need to obtain an estimate for the touched and the touching finger individually and to calculate the distance between them. The rubber-hand illusion is an example in which apparent self-touch overrides the actual spatial discrepancy between the touching finger and the physical hand²⁰⁻²². After a short experience of the rubber hand illusion, the proprioceptive feeling of hand location drifts toward the fake hand^{20,23,24}. In the rubber hand illusion, thus body-part identity dominates the spatial congruency between the visually seen and the proprioceptively felt hand. The three existing studies on spatial tuning of sensory attenuation could all be interpreted as evidence for a determination of self-touch not involving spatial coordinates. In two of these studies^{18,19} subjects could see that they were not touching themselves. In the third study¹⁷, subjects could not see their hands, however, either the index or the middle finger was touched by a motor lever and participants could have based their internal check of self-touch on finger identity.

Here, we asked explicitly whether body part identity or body part position is compared in sensory attenuation of self-touch. We tested sensory attenuation of self-touch in a virtual reality (VR) environment in which we presented 3D arm models such that the touching arm was controlled by the participant's arm movements. Using a VR environment allowed us to manipulate the position of touch in relation to the position where tactile stimulation took place. Participants were asked to touch their left arm with their right index finger (see Figure 2A). The location where to touch their arm was indicated by a small visual spot. When aiming to press their arm, subjects thus would actually touch the device. A hand-held motion controller tracked the location of the pressing finger online. As soon as the motion tracking detected that participants pressed their arm, the mini-vibrating device delivered a short buzz to

mimic the press on the arm. Since subjects were instructed to target their pointing toward the visual spot, we could manipulate whether the visual spot spatially coincided with the physical arm of the subject or not. In the former case, the position of the visual spot in the VR matched the position of the mini-vibrating device on the participants' physical arm. In the latter case, the visual spot in the VR matched the position of an object that was created to provide a similar feeling in the touching finger when touching the arm. In all cases, the mini-vibrating device provided a tactile buzz on the physical arm. In separate sessions, the virtual hand was either visible or not. With these two manipulations (spatial distance between press and touch sensation and visibility of the visual arm), we sought to determine the contributions of the visual and the proprioceptive sense for the localization of the arm during prediction of self-touch.

Results

Spatial estimates between vision and proprioception are precise – Baseline measurement

We first measured the sensitivity to discriminate the location of a visual stimulus against the proprioceptively felt arm location. Subjects were seated in front of a table wearing an HTC Vive Pro headset (see Figure 2A). The participant's physical left arm was resting on the table and was fixated with two plastic loops. Their physical right hand rested on a tracking pad on the right side of the table. All experiments were conducted in a virtual environment - that closely resembled the laboratory room – and participants saw a virtual replica of the table in front of them in the virtual world. In the Baseline measurement, participants were required to judge whether a visual bar stimulus appeared to the left or to the right of their unseen physical arm (see Figure 2B). The bar was oriented parallel to the arm and in each trial, the bar appeared in one of six possible locations. After entering a response with the help of a foot pedal, the next trial started automatically. We estimated psychometric functions with a least square fit and extracted the Point of Subjective Equality (PSE) and the Just Noticeable Difference (JND) for every participant. The average PSE across all participants was $M = 0.05 \text{ cm} \pm 1.48 \text{ (SD)}$, showing that subjects' bias was close to zero, which would equal perfect localization accuracy. The JND of $M = 1.17 \text{ cm} \pm 0.55 \text{ (SD)}$ indicates a precision of 1.17 cm in relating proprioceptive space to visual space. In other words, only within 1.17 cm around the midpoint of their arm, subjects were uncertain when relating the position of a visual stimulus to their arm.

Sensory attenuation for self-touch is replicable in VR – Experiment 1

In Experiment 1, we aimed to replicate the classic sensory attenuation effect for self-touch within our experimental setting. Experiment 1 contained two conditions that were tested in separate sessions: An active pointing and a passive no-movement condition. In the active pointing condition, subjects were seated in front of a table with their physical left and right arms placed in front of them. A vibromotor was attached to the middle of their physical left arm (see Figure 2A). The physical environment was rebuilt within the virtual environment so that in VR participants were seated in front of a virtual table. Both of their arms were presented as visual 3D arm models. After placing the physical hand of participants on a physical trackpad in front of them, a new trial started. Within a trial, subjects were instructed to point at the position of a virtual dot presented on their virtual arm with an active pointing movement. The position of the virtual dot matched the midpoint of their physical arm. When the pointing finger arrived at the position corresponding to that of the virtual dot, a probe vibration occurred on the physical left arm applied by the vibration motor. Subjects had to judge whether the probe vibration appeared weaker or stronger in intensity than a reference vibration which occurred 750 ms later. In the passive no-movement condition, the trial structure remained identical, except that participants did not have to perform an active

pointing movement. Instead, the probe vibration was delivered automatically 1000 ms after the trial start and 750 ms later the reference vibration.

For both conditions, we fitted individual psychometric functions for every participant. In the passive no-movement condition, we found a mean PSE value across participants of $M = 0.12 \text{ [V]} \pm 0.54 \text{ (SD)}$. Thus, a mean of 0.12 volt represents a slight overestimation of the reference stimulus. In the passive no-movement condition, intensity values only slightly deviated from 0. The corresponding average JND of 0.65 [V], with a range of $\pm 0.39 \text{ (SD)}$, suggests a precise discrimination ability in this condition. Comparably, in the pointing condition, participants underestimated the intensity of the probe stimulus with $M_{PSE} = -0.22 \text{ [V]} \pm 0.78 \text{ (SD)}$. We found a significant difference between the PSEs of the two conditions (paired t-test, $t(49) = -2.35$, $p = 0.023$, $d = -0.332$), replicating the classic effect of sensory attenuation. Probe vibrations in the pointing condition, including self-touch, were significantly attenuated compared to the passive no-movement condition.

The discrimination sensitivity in the pointing condition was $M_{JND} = 0.72 \text{ [V]} \pm 0.46 \text{ (SD)}$. Sensitivity was statistically indistinguishable between conditions (t-test, $t(49) = 0.78$, $p = 0.439$). Mean PSE values for the two conditions are shown in Figure 3. The green bar represents the passive no-movement condition, whereas the beige bar represents the active pointing condition.

Visual observation for self-touch generalizes across space – Experiment 2

In Experiment 2, we aimed to spatially dissociate the seen and the proprioceptively felt arm position in an active pointing and a passive no-movement condition. During active pointing trials, participants were asked to conduct the same task as described in Experiment 1. However, in Experiment 2, the virtual dot was randomly positioned at one of three physical locations: the location matching the midpoint on the participants' physical left arm or on one of two fake objects in the physical environment (4 or 6 cm further outward and parallel to the physical arm). The top row of Figure 2C shows the positions of the virtual arm (beige color) relative to the physical hand (shown in black contours). In VR, participants always touched their virtual left arm, whereas physically, depending on the trial, either the physical arm or one of the two fake objects was touched. The virtual arm was displaced in-between trials without participants' notice.

Participants underwent 60 trials for each of the three arm positions. We calculated psychometric functions for all arm positions, for each condition and each participant. Attenuation did not increase between PSEs for the physical arm with $M = -0.21 \text{ [V]} \pm 0.63 \text{ (SD)}$, 4 cm position with $M = -0.25 \text{ [V]} \pm 0.63 \text{ (SD)}$ and 6 cm position with $M = -0.277 \text{ [V]} \pm 0.63 \text{ (SD)}$. The PSEs of the pointing condition are displayed with beige bar plots in Figure 4. The same absence of effects was found for the JND values of the three positions ($F(2, 112) = 0.811$, $p = .447$).

The passive no-movement condition was conducted similarly to the passive condition in Experiment 1. The virtual left arm was visible within the virtual environment, and we presented the visible arm at three positions, matching the physical arm, or the 4 and 6 cm fake object positions from the physical world. The virtual left arm was displaced inconspicuously for participants between trials. As the same subjects in the pointing to a visible arm experiment participated in both, the passive no-movement and the active pointing condition, we conducted a 2x3 repeated measures ANOVA with the factors condition (no-movement vs. pointing) and discrepancy between physical and virtual arm (0, 4, 6 cm). We found no significant effects for the factor position ($F(2, 112) = 0.034$, $p = .966$) and the interaction ($F(2, 112) = 0.475$, $p = .623$). We found a significant effect for the factor condition ($F(2, 112) = 29.072$, $p < .001$), suggesting that attenuation effects were significantly stronger in the pointing condition compared to the passive condition as the probe stimulus was perceived attenuated. Figure 4 shows the discrepancy in attenuation between the two conditions as values of the pointing condition are significantly lower.

Sensory attenuation is spatially tuned in proprioception – Experiment 3

In Experiment 3, we aimed to dissociate the physical and the proprioceptive arm position. Similar to experiments 1 and 2, we conducted an active pointing and a passive no-movement condition. In the active pointing condition, the position of the virtual dot either matched participants' physical arm or one of two fake objects in the physical world (4 and 6 cm shifted to the left of the physical arm). In the virtual environment, the virtual dot was always presented on the virtual arm (see Figure 2C).

Subjects were asked to perform the same active pointing trials as described in Experiments 1 and 2. When participants touched the virtual arm, a probe vibration occurred, followed by a reference vibration 750 ms later. As in Experiments 1 and 2, the task of the subjects was to judge whether the first or second tactile impulse was more intense.

We calculated PSE and JND values for judgments of tactile impulses for each arm position and for each participant. Negative PSE values indicate stronger attenuation. It became evident that attenuation increased when the pointing position was extended further outward. Specifically, the PSE on the physical arm was $-0.14 \text{ [V]} \pm 0.77 \text{ (SD)}$, whereas the shifted 4 cm position led to a PSE of $-0.29 \text{ [V]} \pm 0.66 \text{ (SD)}$ and the shifted 6 cm position to a PSE of $-0.43 \text{ [V]} \pm 0.61 \text{ (SD)}$. This indicates an increase of attenuation as a function of the eccentricity of the pointing position (one-way repeated measures ANOVA $F(1.882, 129.837) = 5.299, p = .007$, due to violation of sphericity Huyn-Feldt results are reported). Barplots showing the mean PSEs of the three conditions can be seen in Figure 5. The x-axis includes the three arm positions. Attenuation for the probe stimulus was strongest at the shifted 6 cm position.

The discrimination ability between the three arm positions did not vary. A one-way repeated measures ANOVA did not reveal a significant effect. Again, as sphericity was violated in the dataset, we report Huyn-Feldt results: $F(1.841, 127.057) = 2.114, p = .129$.

A second sample of participants performed a passive no-movement condition. The subjects felt two tactile vibrations and were asked to judge which tactile impulse was perceived as stronger. The averaged PSE across participants ($M = 0.07 \text{ [V]} \pm 0.622 \text{ (SD)}$) showed a minimal overestimation for the intensity of the probe stimulus. We conducted independent samples t-tests between the PSE of the passive no-movement condition and individual PSEs of all three arm positions to find out whether sensory attenuation was present for all positions. We report Bonferroni-corrected p-values for multiple comparisons. We found significant effects between the passive no-movement condition and the 4 cm shifted position ($t(116) = 2.965, p = .004, d = 0.556$) as well as the passive no-movement condition and the 6 cm shifted position ($t(116) = 4.293, p < .001, d = 0.804$), but not between the passive no-movement condition and the physical arm ($t(116) = 1.564, p = .121$).

Visual observation of self-touch overrides proprioceptive spatial tuning

In order to directly compare the putative dependence of sensory attenuation on the spatial position, we determined the relationship between intensity PSEs and visuo-proprioceptive hand discrepancy. We fitted a linear regression through the individual PSEs values of each participant for the three pointing positions. In Figure 6A linear regressions for two example participants are shown. For sessions in which they had to point to their invisible hand, the relationship between attenuation and hand discrepancy was negative, implying stronger attenuation as a function of hand discrepancy. By contrast, in sessions in which they had to point to their visible hand, the relationship was positive for these two participants.

We extracted slope and intercept values from the linear regression for each participant. Average slopes from pointing to the invisible hand (shown in red) and from pointing to the visible hand (shown in beige) can be seen in Figure 6B. We found a significant effect between the slopes of invisible ($M = -$

0.206 [V] \pm 0.720 (SD)) and visible pointing ($M = 0.058$ [V] \pm 0.653 (SD)): unpaired t-test ($t(125) = -2.142$, $p = .034$, $d = -.382$). Intercept values did not differ significantly ($t(125) = -1.316$, $p = .191$).

Discussion

Voluntary self-touch induces sensory attenuation, i.e., a reduction in apparent tactile intensity^{5,19}. Sensory attenuation is spatially selective and does only occur if the location where a finger is touching an arm and the felt touch position match¹⁷. We asked if such a comparison relies on body-part identity – such that seeing the finger touching the arm suffices to confirm self-touch – or if it takes into account the locations of the touching and the touched body-part. In the latter, the positions of both body-parts must be retrieved and compared. For the touching body-part, an efference copy signal codes the location where and the time when for instance a finger touches the arm. Indeed, in conditions in which no efference copy is generated, sensory attenuation does not occur²⁵.

In the current study, we investigated if proprioception of the touched body-part is compared against the efference copy signal. We asked which signal codes the location of the touch on the arm. Vision and proprioception could both contribute to the estimate of the touch location²⁵. We used a VR environment to manipulate both signals. We presented a virtual visual arm that mimicked the physical arm of the subject. We varied the position of the virtual arm such that it either matched the position of the arm or that it was spatially displaced relative to the physical arm. When subjects could see a virtual arm, we found that sensory attenuation was equally strong, irrespective of a match or mismatch between the virtual and the physical arm. This finding demonstrates that if subjects see both, the touched and the touching arm, the comparison process in sensory attenuation is driven by a simple visual check determining whether the finger actually touches the arm. In other words, if a visual arm is visible the comparison process does not need to estimate the position of the arm since seeing the arm being touched provides sufficient evidence to assume self-touch. Our data show that the visual confirmation of self-touch overrides the need to invoke an extra computation concerning the spatial touch location. In trials in which we did not present a visual virtual arm, we forced the sensorimotor system to use proprioception as the only remaining signal that could tell the location of the touch. Under that condition, we found that sensory attenuation did take into account the mismatch between the physical and the virtual arm. Sensory attenuation grew stronger the bigger the mismatch between the physical and the virtual arm was. The proprioceptive signal was precise because it could distinguish between the three arm positions, but it was not accurate, since it signaled that the arm was more outward than it actually was.

The inaccuracy can be explained by considering how our experimental manipulation affected the proprioception of the arm. In two-thirds of all trials in sessions in which the arm was not visible, they pointed further outward than the physical position of their arm. Yet, when they pointed at the virtual dot, they received tactile feedback on their physical arm. Such a scenario represents a classical sensorimotor conflict^{26–28}. Like in multisensory conflicts^{28–30}, the brain attempts to minimize such conflicts by spatially shifting one of the sensations toward the other³¹. In conflicts involving vision and proprioception, vision is usually dominant and the proprioceptive signal spatially shifts to the visual^{32,33}. The rubber hand^{20,22} and prism adaptation^{34–36} are both examples for the proprioceptive drift. In our paradigm, the sensorimotor conflict must have been resolved by proprioception of the arm shifting further outward. In sessions in which the arm was not visible, sensory attenuation was strongest at the outward position because at that location arm proprioception and the position of the touching arm matched. Sensory attenuation in cases in which the touched body-part location must be retrieved proprioceptively is a true example of spatial tuning. In contrast to the visual check of self-touch, it does process and compare spatial body part information. This process might be important for estimating self-touch in the dark where the visual check cannot be performed.

Sensory attenuation for self-touch must to be distinguished from sensory attenuation for external environment-related stimuli such as sounds generated by a button-press. Arguments have been raised

that these two phenomena rely on different mechanisms⁶. One of these is the spatial tuning of attenuation. In self-touch the action outcome is closely related to the action itself and the sensation can be perfectly predicted. The inclusion of spatial proximity in the comparison of predicted and actual action consequences therefore sharpens the distinction between self- and other-induced sensations. However, for the generation of external stimuli like pressing a doorbell, we can often hardly predict neither the location nor the features of the upcoming sensation. However, studies suggest that for the generation of external stimuli no precise prediction is required. Sensory attenuation was found even if sounds merely coincide unpredictably with a button press^{37,38}. We have recently suggested that tactile motor attention induces sensory attenuation for sounds³⁹.

We conclude that a comparison of both, body part identity and body part position determine sensory attenuation of self-touch. However, the comparison of body part identity is dominant with regard to body part position. No further processing seems necessary if vision confirms that the body part is touched. This way, wasting computational resources will be avoided, since in healthy real-life perception, the visual signal representing a body part is never dissociated from its proprioceptive signal. If the visual signal is unavailable, proprioception delivers an estimate of the respective body part position, which is compared to the efference copy signal, representing the position of the pointing finger. When both signals match in space, sensory attenuation ensues.

Limitations

We conducted our experiments in a VR environment. While we made efforts to maintain a high level of presence and immersion, it remains uncertain how strong participants accepted the virtual hands as their own. The artificial nature of the virtual environment may introduce differences in perceptual processing compared to real-world settings.

Materials and methods

All experimental procedures were carried out in accordance with the ethical standards of the Declaration of Helsinki and were approved by the local ethics committee of the Faculty of Mathematics and Natural Sciences of Heinrich Heine University, Duesseldorf (identification number: 757184). Handedness was assessed using the Edinburgh Handedness Inventory and all participants were classified as right-handers. Participants were recruited at the University of Duesseldorf and were compensated with participation hours or remunerated by means of an expense allowance. Informed consent was obtained from all participants.

General Procedure: Participants were seated in front of a table in a quiet lab environment wearing a VR headset (HTC Vive Pro) and headphones including a noise canceling function (Soundcore Q30). Experiments were conducted on an Alienware Aurora R13 computer (Windows 10, Intel(R) Core(TM) i7-12700F, 2.1GHz, NVIDIA GeForce RTX 3060). The VR setup was implemented within the Steam VR beta (version 1.22.9) software. Using the VR headset, participants were immersed in a virtual environment that closely resembled the physical world. The laboratory, in which the experiment took place, was recreated within VR. Subjects were seated at a virtual wooden table and saw a black window screen in front of them, the trackpad to the right side, their left arm laying on the table, and a movable right virtual arm. Experimental instructions were displayed in red on the black wall in front of participants.

Baseline measurement. In the baseline measurement, 60 participants were tested. One participant had to be excluded because we were unable to fit the data to a psychometric function. For the 59 participants, age ranged from 18 to 32 years, with $M_{Age} = 22.07 \pm 3.29$ (SD), 40 females. 11 had vision correction and all were right-handed.

In Experiment 1, participants were seated in front of a table in a quiet laboratory. Their left arm was fixated on the table with two plastic loops. In VR, participants' hands were not shown, but only the table and the VR environment described in the General Procedure. Participants saw a blue bar (10 cm x 0.5 cm x 5 cm) presented on the virtual table, slightly to the left side of their field of view. Their task was to judge whether the bar appeared to be located to the left or right side of their left real-life arm. The bar was shown at 6 different positions, located parallel to and symmetrically around the physical arm of the subjects (1, 2 or 3 cm to the left or right of the physical hand, see Figure 2B). The physical arm position was calibrated with a Vive tracker positioned in the middle of the arm. Participants entered a response on the foot pedal by judging if the bar was either presented to the left of their arm (left pedal) or the right of their arm (right pedal). The position of the bar was randomized across trials, presented equiprobably at each location with 60 repetitions in total.

Setting for Experiments 1-3. Participants' right hand rested on a grey trackpad with a Vive tracker (HTC Vive Tracker 2.0) mounted on top of a velcro strap attached to their right arm. The Vive tracker was used to track and render participants' right arm in the virtual environment. Participants' left arm was laying on the table, covered by two 3D self-printed plastic loops to prevent participants from changing their arm position. A vibromotor (Adafruit Mini Vibrating Motor Disc Buzzing Motor, 10 mm Diameter), connected to an Arduino nano microcontroller ATmega328 operating at 5 Volt and through a pulse width modulation module (TS-YM-303), was attached on the top of subjects' left forearm using velcro. With the help of a custom-made program in Python (version 3.10.2) and Arduino (Version 1.8.15) we were able to output seven different vibration strengths to the vibration motor by operating at 1.44 V to 4.62 V with 0.53 V differences between levels. During the experiment, participants had to rate vibration intensities. A foot pedal (UPC ECS-PPD-F) was placed under the table so participants were able to respond if the first or second vibration was perceived as stronger. It was randomized between participants whether the first or second vibration referred to the left foot pedal. The experimental setup is shown in Figure 2A.

Stimuli and tasks for Experiments 1-3. During the experiments, participants underwent two different conditions: either a passive no-movement condition or an active pointing condition. In the passive no-movement condition, both arms of the subject rested on the table. A vibromotor was attached to the participants' left forearm.

In the active pointing condition, subjects were seated in front of the physical table with their left arm placed in two plastic loops. After positioning their right hand on the trackpad, a trial started. In the virtual environment, a blue dot (radius: 0.5 cm) appeared 1.5 – 2 seconds after trial start on the subject's left virtual arm. The subjects were instructed to touch the dot with a pointing motion. To control for correct movement execution, the dot turned green (an indicator that the movement was correct) when the pointing criteria were met and could be touched accordingly. A pointing movement was only considered executed correctly if participants' right hand was 15 cm above the table during the peak of the pointing movement. Flat movement executions had to be repeated. When touching the dot, a vibration occurred on the corresponding physical arm position through the vibration motor for 300 ms with an intensity of 3.03 V. 750 ms later, a second vibration appeared, varying in its intensity between six equal distance steps 1.44 V – 2.5 V and 3.56 V – 4.62 V. The same procedure as in no-movement trials was applied: Subjects were asked to decide which vibration felt stronger with the help of the foot pedal, counterbalancing right and left foot buttons. Each stimulus level was presented 10 times, so 60 trials were conducted in total. After the experiments, subjects filled out a custom-made questionnaire where they were asked if anything unusual happened throughout the study or if they felt differences concerning their arm movement.

In the passive movement condition, trials started after participants right hand was placed on the track pad. A probe vibration was presented to participants left arm A reference vibration was presented 750 ms later. Both vibrations lasted 300 ms each. The first vibration (probe) was presented with an intensity of 3.03 V. The second vibration (reference), varied in its intensity between 1.44 V – 2.5 V and

3.56 V – 4.62 V. With the help of the foot pedal, participants were asked to decide whether the first or second tactile intensity was stronger. Pedal pressing was counterbalanced between participants, with either pressing the right button when the first vibration felt stronger and the left button when the second vibration felt stronger or vice versa. After entering their response, the next trial started automatically 1.5 – 2 seconds later. Subjects had to place their right hand on the trackpad during the whole experiment, otherwise, a new trial would not start. Each stimulus level was presented 10 times and 60 trials were conducted in total.

Experiment 1. In Experiment 1, from originally 53 participants, three data sets were excluded from further analysis since their data did not allow to fit a psychometric function. For the final analysis data of 50 right-handed participants between the age of 18 and 34 ($M_{Age} = 21.98 \pm 6.64$ (SD), 28 females) were analyzed. In Experiment 1, participants underwent one passive no-movement and one active pointing condition, as described above. Conditions were presented intermixed between participants.

Experiment 2. For Experiment 2 (including visible passive no-movement and visible pointing condition), we included data from $N = 57$ participants. Three participants had to be excluded from the originally 60 participants as they were able to describe the visual manipulation. Age ranged from 18 to 37 years, with $M_{Age} = 23.17 \pm 4.31$ (SD), 42 females. 15 had vision correction and all were right-handed.

For Experiment 2, we mounted two further vibromotors on top of a custom-made plastic surface, functioning as a fake arm object (in the following referred to as the shifted 4 cm position for the vibromotor position right next to the left arm and the shifted 6 cm position for the furthest vibromotor on the left side). The three vibrating motors were about 2 cm apart from each other and when touching the small vibromotor all three surfaces of the various positions felt identical. Due to the varying width of the subjects' forearms, we had a mean distance between the middle of the subject's left arm and the close fake arm of $d = 4.139$ and between the middle of the subjects' left arm and the far fake arm of $d = 6.103$.

To start a new trial, participants were asked to place their physical right hand on the trackpad in front of them and, in the virtual environment, fixate a blue cross in the upper right corner of their field of view for 500 ms. Next, a blue dot appeared on the left side of their field of view, localized on their left visual arm. Physically, the virtual dot matched either the midpoint of the physical arm, or a position physically shifted 4 or 6 cm.

Participants were asked to touch the virtual dot during the active pointing condition. When touching the green dot, participants felt a probe vibration on their physical arm with a strength of 3.03 V. 750 ms later, participants felt a reference vibration on their arm, varying in six different intensities between 1.44 V – 2.5 V and 3.56 V – 4.62 V. Participants responded by the help of a foot pedal (UPC ECS-PPD-F), by either pressing the left foot pedal if the first stimulus felt stronger and the right foot pedal if the second stimulus felt stronger or vice versa. The order of pedal mapping was randomized between participants. Participants completed two sessions with 90 trials each. During the sessions, the trials were presented randomly on the subjects' physical arm, the 4 cm shifted position, or the 6 cm shifted position, with 10 trials for each vibration strength for each position, resulting in 180 trials in total.

After each trial, the participants were asked to fixate on a blue cross in their top right visual field of view. Following the fixation, a black screen was flashed for 500 ms, during which the position of the visual left arm was shifted. During fixation, the left arm was outside the participants' field of view, so the visual arm shift took place unobtrusively. As we varied the visual arm position between trials, participants always had the visual feedback of touching their virtual arm. Physically, they touched the 4 cm and 6 cm shifted fake objects in 33.3% of cases each. At the end of the experiment, participants were asked in a questionnaire if they noticed the arm shift. Based on their responses, three participants were excluded from the analysis. Participants completed both, the passive no-movement condition and the active pointing condition.

Experiment 3. In Experiment 3 we tested $N = 70$ participants in the invisible pointing condition. Their age range varied between 16 and 52 ($M_{Age} = 22.09 \pm 7.8$ (SD), 28 females). 18 participants had vision correction in the form of glasses or contact lenses, and all were right-handed. In the invisible

passive no-movement condition, we analysed data of $N = 48$ participants (age range: 19 to 36, $M_{Age} = 24.01 \pm 5.5$ (SD), 32 females, 9 with vision correction). Experiment 3 was identical to Experiment 2 except that during the passive no-movement and active pointing condition, the virtual left arm was invisible in VR. To start a new trial in the active condition, participants were asked to place their physical right hand on the trackpad in front of them and fixate a blue cross in the upper right corner of their field of view for 500 ms. Next, a blue dot appeared on the left side of their field of view, localized either on their arm, the shifted 4 cm position in the physical world, or the shifted 6 cm position in the physical world. The left virtual arm was invisible, so targets were only presented at the same height as the upper part of the left arm. The height was measured in a calibration phase at the beginning of the experiment. We also measured a passive no-movement condition in this experiment, as described in the section *Stimuli and tasks for Experiments 1-3*. Participants were seated and asked to judge the intensity of two vibrations presented to their left arm. The virtual left arm was invisible in this condition.

Data analysis. Data preprocessing was performed in RStudio (Version 1.4.1103). We calculated mean correct responses per stimulus level and estimated psychometric functions with a least square fit in RStudio (Version 1.4.1103). Statistical analysis was performed in JASP 0.16.3 (Intel).

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Author Contributions

M.B. and C.F. contributed equally to this paper. M.B. programmed the study environment, C.F., M.B., and E.Z. designed and performed research, C.F. analyzed data, C.F., M.B., and E.Z. wrote the paper.

Data availability statement

Data and code to reproduce analyses have been deposited in OSF available at <https://osf.io/k9nuz/>

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Declaration of interests

The authors declare no competing interests.

Classification: Biological Sciences, Psychological and Cognitive Sciences

Keywords: Sensory attenuation, spatial tuning, self-touch

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Temporal adaptation of sensory attenuation for self-touch

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Abstract

The sensory consequences of our actions appear attenuated to us. This effect has been reported for external sensations that are evoked by auditory or visual events and for body-related sensations which are produced by self-touch. In the present study, we investigated the effects of prolonged exposure to a delay between an action and the generated sensation on sensory attenuation for self-touch. Previously, it has been shown that after being presented to a systematic exposure delay, artificially delayed touch can feel more intense and non-delayed touches can appear less intense. Here, we investigated the temporal spread of the temporal recalibration effect. Specifically, we wondered whether this temporal recalibration effect would affect only the delay that was used during exposure trials or if it would also modulate longer test delays. In the first two experiments, we tested three test delays (0, 100 and 400 ms) either in randomized or in blocked order. We found sensory attenuation in all three test intervals but no effect of the exposure delay. In Experiment 3, we replicated the experiment by Kilteni et al. (ELife 8:e42888, 2019. <https://doi.org/10.7554/eLife.42888>) and found evidence for temporal recalibration by exposure delay. Our data show that the temporal selectivity of sensory attenuation of self-touch depends on presenting a singular test delay only. Presenting multiple test delays leads to a temporally broad spread of sensory attenuation.

Keywords Sensory attenuation · Efference copy · Self-touch · Temporal adaptation

Introduction

Imagine moving your right finger to touch your left arm. Even before your finger makes contact, your brain knows what you are going to sense. Sensorimotor predictions lead to a decrease in the perceived intensity of touch, a phenomenon termed sensory attenuation (Blakemore et al. 1998, 1999). The most prominent example for sensory attenuation is the inability to tickle ourselves. Self-produced touches are perceived as weaker or less intense than externally produced touches (von Holst and Mittelstaedt 1950). The standard theory of sensory attenuation is the comparator model that relies on the movement generation architecture provided by classical control theory (Blakemore et al. 2000, 2002). In this scheme, a movement plan is constructed by an inverse model. The movement plan is sent to the motor plant in order

to relay a movement command to the muscles. A copy of the movement plan, the so-called efference copy is used to compute a forward model that entails a prediction of the sensory consequences following the planned movement. When the movement is finished, the predicted and the actual sensory consequences are compared. If the prediction matches the actual consequences, the sensation is attenuated (Bays et al. 2005, 2006, 2008; Witney et al. 1999; Wolpert and Flanagan 2001).

Kilteni et al. (2020) demonstrated that sensory attenuation only occurs when performing an active, compared to a passive self-generated touch. In their experiment, participants were asked to actively press a force sensor with their right index finger after hearing an auditory go signal. The press resulted in a lever touching the top of their left index finger. In a second condition, participants placed their right index finger on a plastic surface, located above the force sensor for the right index finger. When the auditory go signal occurred the plastic surface vanished, causing participants finger to fall freely onto the underlying sensor. Again, this tap resulted in a lever touching the top of their left index finger. Although the contact by the lever was self-generated and predictable in both conditions, sensory attenuation was

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only evident in the active condition. In addition, the extent of the perceived intensity of the lever pressure in the passive condition was comparable to that of an externally generated contact. The authors concluded that an active, self-generated movement produces an efference copy that is responsible for the attenuation effect of self-contact. In accordance with the comparator model the findings suggest that a small prediction error (coupled with a higher accuracy of prediction) will lead to a less intensely perceived touch compared to a touch resulting from an external movement (Blakemore et al. 1998; Fraser and Fiehler 2018; Voudouris and Fiehler 2017, 2021). Importantly, touch is spatially selective for the goal location of the touching movement (Bays et al. 2008; Kilteni and Ehrsson 2017; Knoetsch and Zimmermann 2021). Such a precision requires that the mechanism, inducing sensory attenuation, takes into account a detailed description of the positions of body parts.

If systematic changes in the timing between a motor action and the corresponding sensory feedback occur, the sensorimotor system adapts (Cunningham et al. 2001; Heron et al. 2009; Rasman et al. 2021). This recalibration process has been studied by asking subjects to judge the temporal order between a button press and a flash (Stetson et al. 2006). When the authors injected a fixed delay, temporal order judgements shifted toward the injected delay. A following study determined that it is the motor component which temporally shifts toward the perceptual event (Sugano et al. 2010). Adaptation to temporal delays between action and perception has also been investigated in the multi-sensory domain. Data have suggested that auditory feedback for motor-sensory temporal recalibration is more likely to occur than for visual feedback (Sugano et al. 2016). Furthermore, recalibration transferred from vision to audition but not vice versa (Arikan et al. 2021). Other studies found that performing actions widens the window of multi-sensory simultaneity, irrespective of whether the movement is voluntary or involuntary (Arikan et al. 2017). The window of audio-visual simultaneity can be increased when participants learn that the delay between action and audio-visual pair is variable (Desantis and Haggard 2016). Results from our lab have recently shown that the strength of sensory attenuation for visual events is modulated by injected delays between action and perception (Storch and Zimmermann 2022).

Kilteni et al. (2019) asked whether temporal recalibration could also be demonstrated for sensory attenuation for self-touch. In their experiment participants had to touch a force sensor with their right finger in order to rotate a lever to tap their left finger. A systematic delay of 0 ms or 100 ms (exposure delay) was inserted between the voluntary tap of the right index finger and the resulting touch on the pulp of the relaxed left index finger. After exposing subjects for 500 trials to a 0 ms delay between button press and lever touch, they found sensory attenuation in test trials when the

lever touch followed immediately after button press (0 ms test delay), but not when it followed 100 ms later (100 ms test delay). The crucial condition contained an exposure of 500 trials to a delay of 100 ms between button press and lever touch. In these sessions, subjects were supposed to learn a new temporal sensorimotor contingency between button press and the time of the ensuing tactile sensation. After being exposed to the 100 ms exposure delay, subjects showed no sensory attenuation in test trials, which contained 0 ms between button press and tactile sensation (test delay 0 ms). This absence of sensory attenuation was interpreted by the authors (Kilteni et al. 2019) as unlearning of sensory attenuation. In contrast, subjects were able to learn attenuated touch based on the predicted delay of 100 ms.

Here, we sought to investigate first whether temporal recalibration leads to attenuation of touches presented at the same test delay as the exposure one or if attenuation will be observed for touches presented at other delays too. In the latter case, prolonged exposure to a delay in self-touch might also be observable in test delays which are longer than the exposure delay. Second, we asked if the predictability of an experimental condition e.g., a learned test delay of 0 ms or 100 ms, might influence the ability of learning a prolonged delay. We asked whether blocked versus randomized presentation of test delays show different effects. To investigate this hypothesis, we tested our introduced test delays of a non-movement baseline, 0 ms, 100 ms and 400 ms in a randomized and separately in a blocked order. We expected that the effects of temporal predictability would no longer occur, when comparing sensory attenuation magnitudes for different probe delays. We also conducted a replication of one of the experiments by Kilteni et al. (2019).

Methods

Participants

Participants were recruited in the University Düsseldorf, by personal contacts or via social networks. All experiments were in accordance with the Declaration of Helsinki and were approved by the local ethics committee of the Faculty of Mathematics and Natural Sciences of Heinrich Heine University, Düsseldorf (Identification No. 757184). Handedness was assessed using the Edinburgh Handedness Inventory and written informed consent was obtained. Participants were compensated with participation hours or remunerated by means of an expense allowance.

Experimental setup

Participants were seated in front of a table in a quiet room with the apparatus placed in front of them. Participants

placed their left hand in an upside-down position approximately 5 cm underneath a motor (Savöx SC-1257 TG). The motor was mounted underneath a metal arc with the help of double-sided adhesive tape. The left index finger was touched by the motor only when moving the lever. To keep the left forearm and hand comfortable bubble wrap was used. The right hand laid on top of the metal arch with the right hand resting above of a force sensor (FSR®, Interlink Electronics, Inc, Camarillo, CA 93012, USA). Participants were instructed to press the force sensor with their right index finger only.

In exposure trials, the apple system sound “Funk” was used as the auditory go signal (duration: 510 ms, frequency: 44.1 kHz). In test trials, a tom tom drum sound was used (duration: 250 ms, frequency: 44.1 kHz). After pressing the force sensor, the motor’s lever simulated a finger touch to the left index finger. The motor was controlled by a custom-made Objective-C program, by sending commands via the serial port to the micro-controller (Arduino Nano Atmega328 CH340). The Arduino Nano was connected to a MacBook Pro (Retina, 15-inch, 2015). Since information within the micro-controller is processed in the micro-seconds range, the delay between force sensor presses and motor rotation is mostly produced by the regulating time of the motor. The Savöx SC-1257 TG when used at 4.8 V (in our study 5 V was used) has a regulating time of 90 ms/60°. We let the motor rotate the connected lever by 20°. There was thus an approximate delay between button press and lever rotation of 30 ms. The duration of a tactile stimulation was 270 ms in Experiment 1 and 2 and 100 ms in Experiment 3. The experimental setup can be seen in Fig. 1.

During the experiments, we differentiated between exposure trials and test trials. In exposure trials, subjects heard an auditory go signal which indicated to press the force sensor. After pressing, the lever rotated with a delay of either 0 ms or 100 ms to simulate a touch on participant’s left index

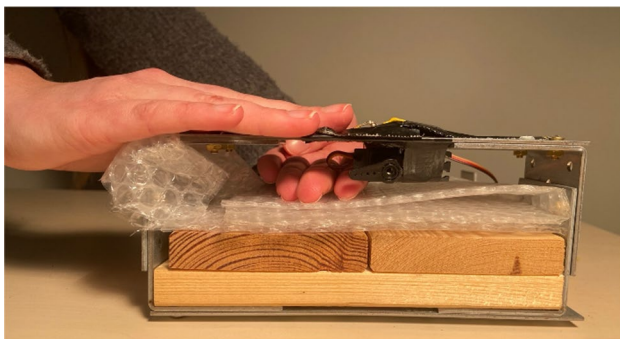


Fig. 1 Experimental setup. The left hand was placed underneath the motor which was attached to a metal arch. Once the auditory go signal occurred, participants were instructed to press the force sensor with the right index finger which led to the left index finger being touched by a lever controlled by the motor

finger. In test trials, subjects heard a different auditory go signal (tom tom drum) to sensitize them for a response. During test trials, the lever rotated two times after the force sensory was pressed. The first rotation (probe touch) occurred with either – 100 ms (baseline), 0 ms, 100 ms or 400 ms delay (depending on the experiment). The second rotation (reference touch) occurred automatically 1500 ms after the probe touch. Participants were asked to indicate whether the first or the second touch felt stronger. Therefore, we used two-alternative forced choice (2AFC), so participants were forced to decide between the stimuli. Responses were made by the help of a foot pedal (UPC ECS-PPD-F) placed under the table.

Experiment 1

In Experiment 1, we tested 36 participants (15 male, 21 female). Two of them were left-handed and their age ranged from 18 to 37 years ($M = 25.63$).

The experiment started with 500 exposure trials. 1000 ms after trial start an auditory cue (Apple System Sound) indicated to press the force sensor. Once the micro-controller detected that the force sensor was pressed, the lever was rotated by the motor and touched the subjects right index finger with a strength of subjectively perceived 2 N. Depending on the exposure delay, the rotation occurred either simultaneously with the press or 100 ms later. Exposure delays were tested in different sessions. Thus, in Experiment 1, participants had to perform two sessions: either with an introduced exposure delay of 0 ms or 100 ms. We randomized the order of sessions.

In test trials, the auditory go signal consisted of a tom tom drum sound. When pressing the force sensor during a test trial, the lever rotated two times. The rotation of the first, the probe touch, occurred either simultaneously with the press or after a certain delay (test delay). The test delay varied between conditions, with the lever rotating either 100 ms before the auditory signal (baseline), directly with the force sensory press (0 ms), 100 ms or 400 ms after the force sensory press. In the baseline condition, participants did not have to press the force sensor to trigger a movement of the motor. 100 ms before the auditory go signal occurred, the lever rotated automatically. The four conditions (baseline, test delay 0, 100 and 400 ms) were presented in randomized order for each of the two exposure delays. The 0 ms and the 100 ms exposure delays were measured in separate sessions.

After the probe touch, a second, the reference touch occurred 1500 ms later on the same finger. As stated above participants were forced to decide which touch felt stronger (2AFC). When participants gave their response, the next trial started immediately. Each test trial was followed by 5 exposure trials, then the next test trial was presented again. In Experiment 1, we had 80 test trials in total. As

one experimental session started with 500 exposure trials, followed by 1 test trial and 5 exposure trials again, we had a total of 980 trials in each session. As stated above, for Experiment 1, two sessions were performed, so we had a total of 1960 trials. The temporal outline of the exposure and test delays can be seen in Fig. 2.

An adaptive staircase procedure (Best PEST) was used to estimate the perceived equality of probe and reference touch (Pentland 1980). The Best PEST method is an adaptive method of psychophysics for determining the perception threshold of a subject to a stimulus. In our experiment, threshold estimation was conducted between subjectively perceived 1.7–2.3 N in steps of 0.1 N. Subjectively perceived N values for the applied motor force were determined with the help of a short pilot testing in advance to testing experiments. We asked a different data set of participants to press the force sensor with their right index finger. The intensity of the press was read out by the connected micro-controller and displayed on the computer. We could thus assess the exact force applied during pressing. For each a priori determined increment between 1.7 and 2.3 N, subjects were asked to press the sensor with

the corresponding strength. After an individual training period, subjects were able to follow instructions. For each press the motor lever provided a certain force on the left index finger of the subjects. They could adjust the force of the motor gradually until they were confident that it matched the force of their press. Progression of the pressed strength and the output received is linear. With this procedure, we could produce an average mapping between the a priori defined increments (1.7–2.3 N) and the subjectively determined forces that the motor has to apply. After pilot testing, we averaged subjectively perceived values that were used as standard values across participants for the following experiments. The values remained identical except for differences between Experiment 1 and 2 versus 3. The presentation of the next stimulus increments depended on the subject's previous response. Participants used the foot pedal to indicate which of two stimuli felt stronger. Based on this response, the subsequent stimulus was adjusted. If the previous response resulted in a stronger perception of the stimulus, the subsequent stimulus strength was adjusted correspondingly lower. Conversely, if the previous response reported a weaker perception of the stimulus,

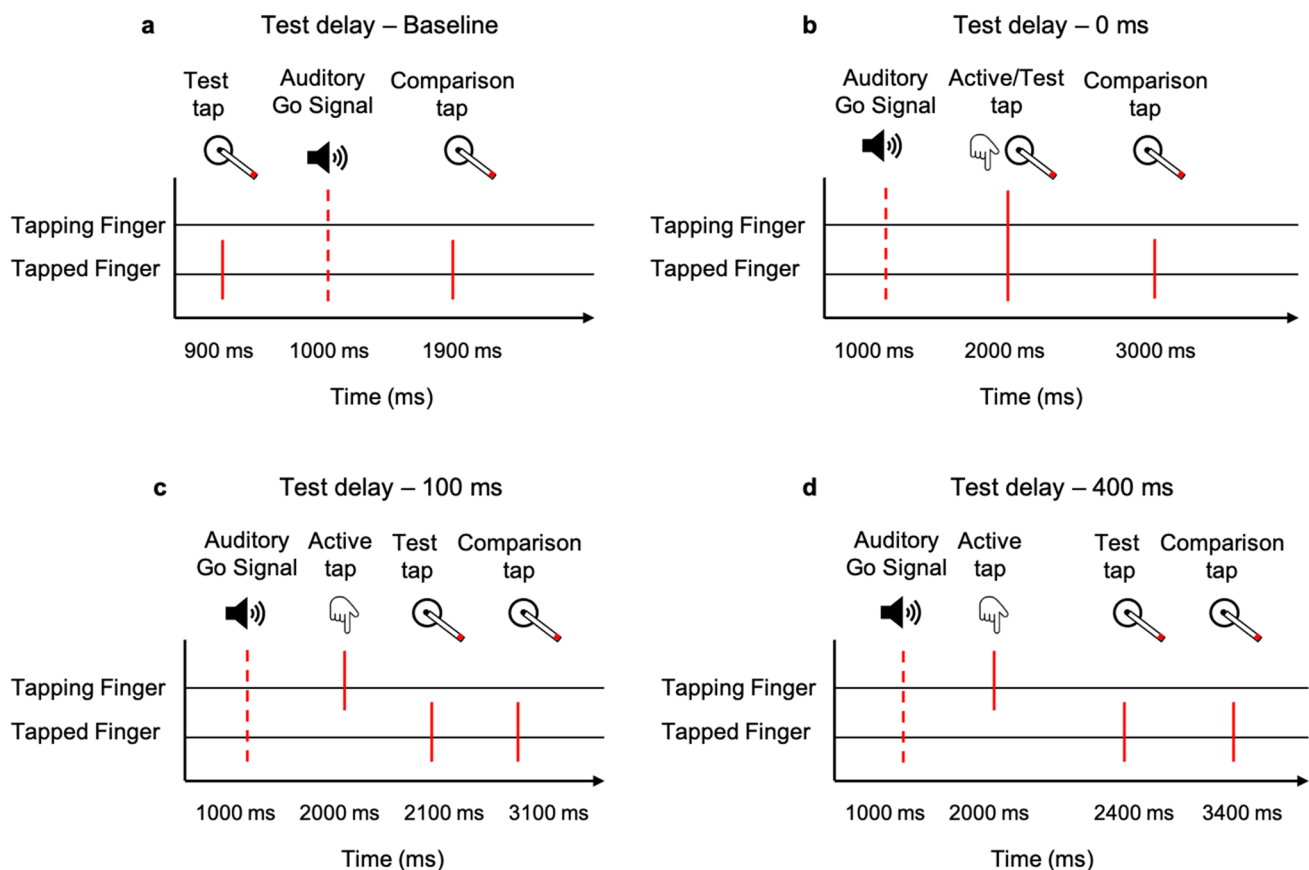


Fig. 2 Temporal outline of test delays in Experiments 1 and 2. Participants heard an auditory go signal via headphones, indicating them to press the force sensor. During test trials, the delay between active

tap and test tap varied between 0, 100, 400 ms or no active tap had to be conducted to receive a test tap baseline). The comparison tap occurred 1500 ms after the test tap.

the subsequent stimulus strength was increased. Thus, the stimulus strength adapts to a threshold over time.

As the Best PEST method offers an adaptive parameterization of stimuli, this method increases accuracy and the elimination of systematic errors. Less trials for the analysis are needed, reducing the number of stimulus presentations and thus the duration of the experiment (Lieberman and Pentland 1982).

Experiment 2

In Experiment 2, we collected data of 40 participants. Two subjects had to be excluded due to wrong task execution. Therefore, in the analysis, we included 38 subjects (16 male, 21 female, 1 diverse) with a mean age of $M = 24.79$ and age ranging from 18 to 36 years. Three subjects were left-handed.

The methodological structure of Experiment 2 was similar to Experiment 1. Again, subjects were asked to conduct two sessions, with a presented exposure delay of either 0 or 100 ms in the exposure trials. It was randomized which exposure delay occurred first. Though, here the four test delays (baseline, 0 ms, 100 ms, 400 ms) were presented block-wise. In Experiment 1, the test delays were presented randomly, whereas in this experiment, the same test delay was presented for 20 test trials. Otherwise, the trial structure remained similar to Experiment 1: at the beginning, 500 exposure trials were presented. Afterwards, one test trial was followed by 5 exposure trials again. For every test delay, 20 test trials were presented, so we had 80 test trials in total, having 980 trials in total per session. As participants had to conduct one session with an exposure delay of 0 ms and one with an exposure delay of 100 ms, 1960 trials were conducted per participant.

Experiment 3

Experiment 3 included data of 36 participants. We tested 9 male and 27 female with a mean age of $M = 24.66$ and age ranging from 18 to 37 years. The task as well as the exposure delays in Experiment 3 were identical to Experiment 1 and 2. Sessions were conducted with an exposure delay of either 0 ms or 100 ms. For the test delays, we included only 0 ms and 100 ms. Experiment 3 contained 4 conditions: an exposure delay of 0 ms and a test delay of 0 ms/100 ms or an exposure delay of 100 ms and a test delay of 0 ms/100 ms. We measured every condition in a separate session, so participants had to complete 4 sessions in total in Experiment 3. The order of conditions was randomized between test subjects. In Experiment 3, a psychometric function with 7 constant stimuli was measured. The probe touch had a strength of subjectively perceived 2 N. To this end, the strength of the second reference touch

by the lever in a given trial was chosen randomly out of 7 possible reference magnitudes (subjectively perceived 1.4–2.6 N in 7 equidistant steps). For every reference magnitude, 10 test trials were presented. Tactile stimulation lasted 100 ms. Every test trial was followed by 5 exposure trials. The experiment started with 505 exposure trials and participants had to complete 70 test trials and 350 extra exposure trials.

Power analysis

A statistical power analysis was performed for sample size estimation, based on data from Kiltner et al. (2019) ($N = 30$). The effect size in the study of Kiltner et al. (2019) varied between conditions (ranging from 0.343 to 0.848). As we were looking predominantly on the classical effect of expected versus unexpected delays, we conducted a power analysis for the effect sizes of the paired t -test between (exposure delay: 100 ms, test delay: 100 ms) and (exposure delay: 0 ms, test delay: 100 ms): $t(29) = -3.29$, $p = 0.003$, $CI^{95} = [-0.142, -0.033]$, $d = 0.601$. With an $\alpha = 0.05$ and power = 0.95, the projected sample size needed with this effect size is approximately $N = 38$. Thus, our proposed sample size should be adequate for the main objective of this study and should also allow for expected attrition.

Results

Data analysis

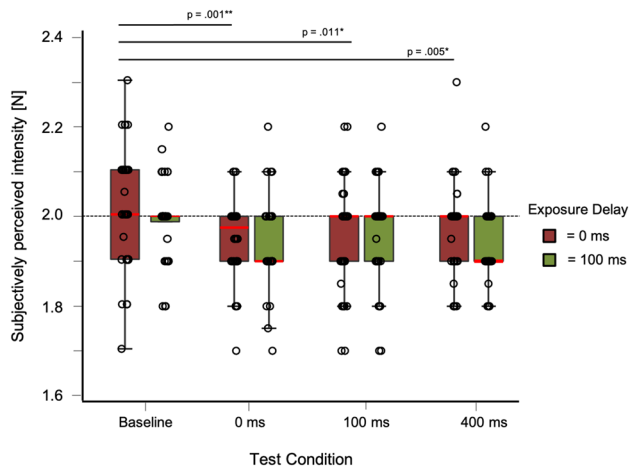
Since the Best PEST method uses an adaptive threshold procedure, participant's individual perceived intensity of touch [N] is revealed towards the end of the test trials. We used 20 test trials for each threshold determination and used the last 5 values to calculate thresholds. In Experiments 1 and 2, four thresholds were measured per session per condition (for baseline, 0 ms, 100 ms, 400 ms). Since we conducted two sessions in each experiment to test the different exposure delays (0 ms, 100 ms), this resulted in eight thresholds per subject in the respective experiment.

For Experiment 3, data were fitted by a cumulative Gaussian function for each condition and test delay per participant (cumulative Gaussian function, $\text{fcn} = @ (b, x) \text{normcdf}(x, b(1), b(2)); \text{NRFCF} = @ (b) \text{norm}(Y/100 - \text{fcn}(b, X)); B = \text{fminsearch}(\text{NRFCF}, [0; 10])$, fitted in MATLAB_R2020b). The point of subjective equality (PSE) represents the magnitude at which the probe tap is perceived as stronger than the comparison tap on 50% of the trials.

Data were analyzed in JASP 0.16.3 and MATLAB_R2020b.

Table 1 Mean and standard deviation for test trials in Experiment 1

Exposure delay (ms)	Test delay							
	Baseline		0 ms		100 ms		400 ms	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
0 ms	2.02	0.13	1.95	0.09	1.96	0.12	1.96	0.10
100 ms	1.99	0.09	1.95	0.10	1.96	0.11	1.95	0.09

**Fig. 3** Box-and-whisker plots for Experiment 1. Tests conditions are shown against subjectively perceived intensity [N] including individual data points. Red bars for each condition represent the median

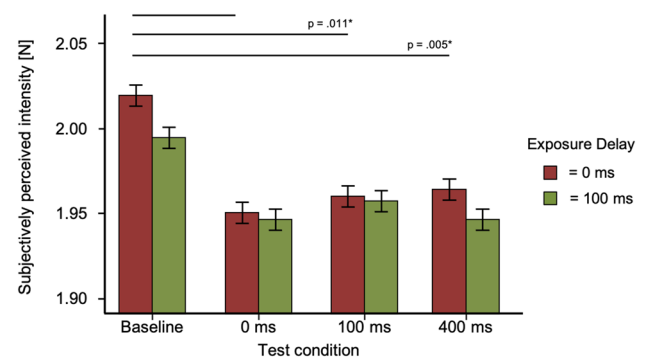
Experiment 1

For Experiment 1, we estimated the subjective intensity [N] of a self-touch with an adaptive staircase method (Best PEST). Estimated intensity values were then averaged for each condition across all subjects. A repeated-measures 2×4 ANOVA was conducted to identify whether the conditions were significantly different from each other. The ANOVA included the two factors exposure delay (with levels 0 ms and 100 ms) and test delay (with levels of four test delays [Baseline, 0 ms, 100 ms, 400 ms]).

Descriptive statistics for the test trials can be found in Table 1 and distribution of data in Fig. 3.

The repeated-measures ANOVA showed no significant effects for the factor exposure delay ($F(1, 35) = 0.819$, $p = 0.372$). As the Mauchly-Test was significant, the Greenhouse–Geisser adjustment was used to correct for violations of sphericity in the condition test delay and the interaction. All other requirements for parametric testing were met. The interaction showed no significant effect ($F(2.65, 35) = 0.39$, $p = 0.76$). For the factor test delay, we found a significant effect ($F(2.36, 35) = 6.27$, $p = 0.002$).

A post hoc analysis for the factor test delay (tested against a Bonferroni-adjusted alpha level of 0.05/6) revealed that

**Fig. 4** Results of Experiment 1. Bar plots for every exposure and test trial. Tests conditions are shown against subjectively perceived intensity [N]. Error bars represent standard errors (s.e.m.)

there was a significant difference between the test delay of baseline and 0 ms ($MD = 0.06$, $SE = 0.02$, $p = 0.001$, $d = 0.646$) as well as a test delay of baseline and 100 ms ($MD = 4.86$, $SE = 1.523$, $p = 0.011$, $d = 0.532$) and baseline and 400 ms ($MD = 5.21$, $SE = 1.523$, $p = 0.005$, $d = 0.570$). p values are Bonferroni corrected ($p/6$). No significant effects were found between the other delays ($p > 0.81$). Distribution of data between test conditions for Experiment 1 is shown in Fig. 4.

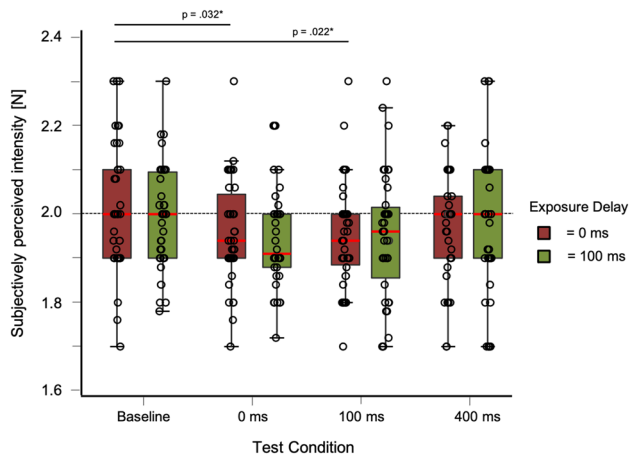
In Experiment 1, test conditions were randomized within each session so timing of the presented test delay was not predictable. In order to test whether the absence of effects of the exposure delay occurred due to the missing temporal predictability, we conducted a second experiment in which we presented the test intervals in four fixed blocks.

Experiment 2

In Experiment 2, we presented test trials in a blocked order. Each test delay was presented for 20 test trials in total, intermixed with 5 exposure trials after each test trial. The order of test delay blocks was counterbalanced across participants. As the overall method remained identical, we conducted the same steps for data analysis as in Experiment 1: the last 5 stimuli values for each test and exposure delay per participant were averaged. We also conducted a repeated-measures 2×4 ANOVA (factor one: exposure delay of 0 ms and

Table 2 Mean and standard deviation for test trials in Experiment 2

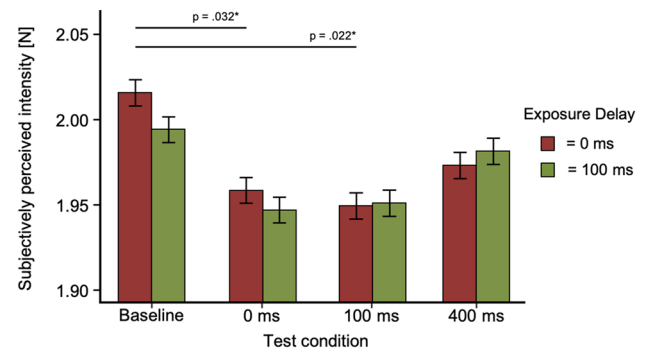
Exposure delay (ms)	Test delay							
	Baseline		0 ms		100 ms		400 ms	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
0 ms	2.02	0.15	1.96	0.12	1.95	0.12	1.97	0.13
100 ms	1.99	0.12	1.95	0.12	1.95	0.15	1.98	0.16

**Fig. 5** Box-and-whisker plots for Experiment 2. Tests conditions are shown against subjectively perceived intensity values [N] including individual data points. Red bars for each condition represent the median

100 ms, factor two: test delays of baseline, 0 ms, 100 ms, 400 ms) and used paired sample *t*-tests for comparison between baseline and the other conditions. The mean and standard deviation for the different exposure and test delays are shown in Table 2. Figure 5 shows distribution of data for the conditions.

As the Mauchly-Test was significant, the Greenhouse–Geisser adjustment was used to correct for violations of sphericity in the condition test delay and the interaction. All other requirements for parametric testing were met. The ANOVA showed a significant main effect for the factor test delay ($F(3, 37) = 3.86, p = 0.016, \eta_p^2 = 0.041$). For exposure delay ($F(3, 37) = 0.095, p = 0.76$) and exposure delay \times test delay ($F(3, 37) = 0.359, p = 0.777$) no significant effects were found. A post hoc analysis revealed that there was a significant difference between the test delay of baseline and 0 ms ($MD = 0.05, SE = 0.18, p = 0.032, d = 0.396$) as well as a test delay of baseline and 100 ms ($MD = 0.06, SE = 0.18, p = 0.022, d = 0.414$). *p* values are Bonferroni corrected ($p/6$). No significant effects were found between the other delays ($p > 0.817$). Figure 6 shows an overview of results.

We found weaker effects between conditions compared to Experiment 1. We aimed to rule out that differences to the results of the original study of Kilteni et al. (2019) were

**Fig. 6** Results of Experiment 2. Bar plots for every exposure and test trial. Tests conditions are shown against subjectively perceived intensity [N]. Error bars represent standard errors (s.e.m.)

due to the choice of the threshold estimation method. Kilteni et al. (2019) used psychometric functions, whereas we used an adaptive staircase (Best PEST) procedure. To this end, we measured subjects with psychometric functions as well and conducted a conceptual replication of Kilteni et al. (2019).

Experiment 3

In Experiment 3, we tested the same conditions as in Kilteni et al. (2019). Data were analyzed with psychometric functions seen in Fig. 7. Similar to the other experiments, the exposure delay differed between no delay (0 ms) and 100 ms delay during exposure trials. The factor test delay differed between a 0 ms or 100 ms delay of the test touch after the force sensor press. Mean and standard deviation for PSE and JND of the experiment are shown in Table 3. Data distribution is shown in Fig. 8.

As the requirements for parametric testing were met, we conducted a 2×2 repeated-measures ANOVA (factor one: exposure delay of 0 and 100 ms, factor two: test delay of 0 ms and 100 ms). No significant effects for either the factor exposure delay ($F(1, 35) = 0.063, p = 0.803$) nor test delay ($F(1, 35) = 1.783, p = 0.190$) were found. The interaction between exposure delay and test delay was significant ($F(1, 35) = 4.869, p = 0.034$). Bar plots can be seen in Fig. 9.

Since the authors in the original study of Kilteni et al. (2019) used a priori planned paired *t*-tests to compare effects of sensory attenuation between conditions, we

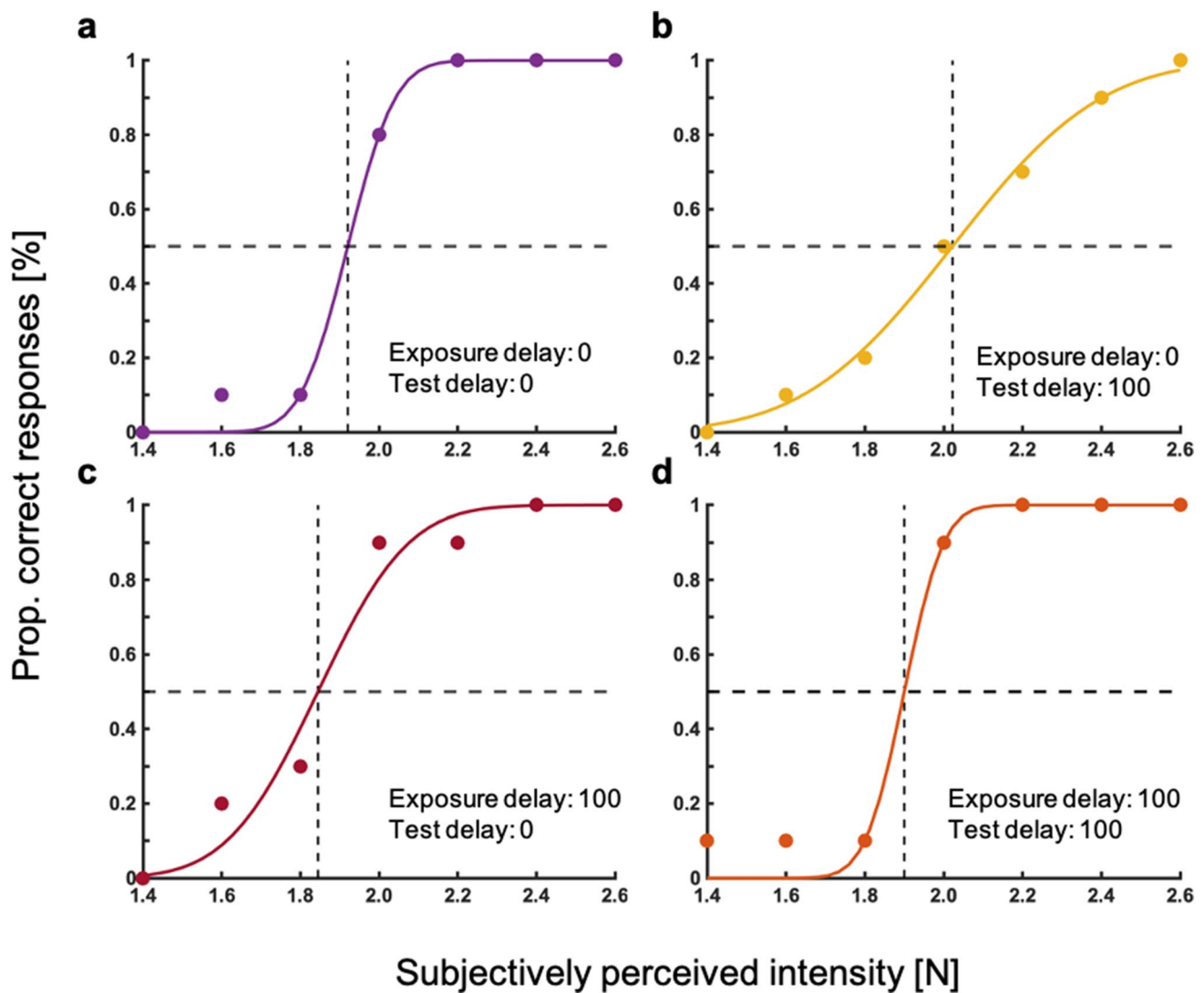


Fig. 7 Psychometric functions of an example participant for the four conditions. Proportions of correct responses are shown against the perceived intensity of second touch

Table 3 Mean and standard deviation for PSE and JND in Experiment 3

Exposure delay (ms)	Test delay							
	0 ms (PSE)		100 ms (PSE)		0 ms (JND)		100 ms (JND)	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
0 ms	1.92	0.10	1.97	0.09	0.25	0.14	0.23	0.13
100 ms	1.95	0.13	1.93	0.13	0.23	0.12	0.26	0.13

checked our data for the effect of classical sensory attenuation with this analysis method. We conducted a paired sample *t*-test between the test conditions of an exposure and test delay of 0 ms compared to an exposure delay of

0 ms and a 100 ms test delay ($t(35) = -2.86$, $p = 0.007$, $d = 0.476$).

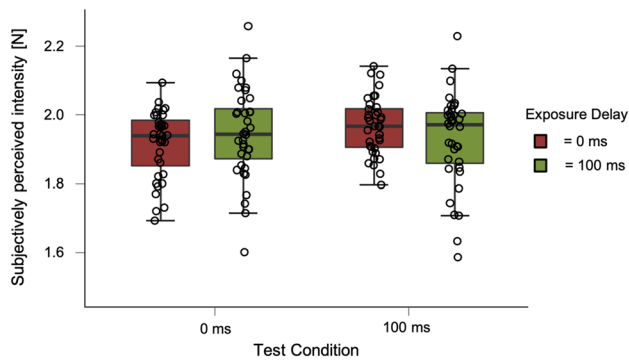


Fig. 8 Box-and-whisker plots for Experiment 3. Tests conditions are shown against subjectively perceived intensity [N] including individual data points. Black bars for each condition represent the median

Discussion

In this study, we asked about the spread of temporal recalibration in sensory attenuation of self-touch. When participants are asked to touch their left with their right finger and, by means of an experimental device, are exposed over several trials to a delay (100 ms) between their touch and the ensuing tactile sensation, sensory attenuation shifts in time to the exposed delay (Kilteni et al. 2019). Furthermore, sensory attenuation disappeared when self-touch was tested without a temporal delay. These data are consistent with a temporal recalibration mechanism which adapts the internal prediction of the time when actions yield sensory consequences.

We wondered whether temporal recalibration would tightly couple sensory attenuation to the newly learned delay (100 ms) or if it would spread more broadly when tested in longer intervals. The first possibility would be in line with a very precise temporal recalibration whereas the latter would argue for a shift of the entire tuning curve of sensory attenuation. Previous research investigating the time-course of sensory attenuation of self-touch found that the decrease in perceived tactile intensity starts 300 ms before the active right finger touches the passive left finger and returns to baseline level about 300 ms after it (Bays et al. 2005). We reasoned that adaptation to a delay between the active touch and the passive tactile sensation might shift this tuning curve rather broadly such that sensory attenuation could even be measured at longer delays. To this end, in our first two experiments, we tested three temporal delays (0, 100 and 400 ms) after separate exposure delays of 0 ms and 100 ms. In Experiment 1, these test intervals were randomly interleaved between exposure trials. The ratio of the number of exposure and test trials was identical to previous studies (Stetson et al. 2006; Kilteni et al. 2019). To our own surprise, we found sensory attenuation in all test delays

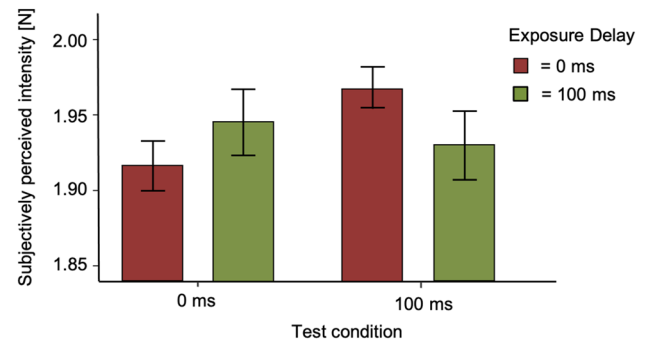


Fig. 9 Results of Experiment 3. Bar plots for the two test conditions and exposure delays. Tests conditions are shown against subjectively perceived intensity [N]. Error bars represent the standard error of the mean

and no effect of the exposure delays. In order to rule out that the randomly interleaved presentation of three different test delays might have led to this broad spread of sensory attenuation, we conducted a second experiment, in which we blocked the presentation of test delays. The data in this experiment were similar to the first experiment.

To better understand these results, in our Experiment 3, we replicated the study by Kilteni et al. (2019). Our methodological setup differs from that of Kilteni et al. (2019) in some aspects: first, we deviated slightly from the way physical force values were selected in Kilteni et al. (2019). As outlined in “Methods”, our force value selection was based on subjectively perceived estimates rather than physical force intensities. Second, we were unable to directly measure the actual applied intensities and thus could not re-bin trials based on the force measured on the left index finger. In a follow-up study (see supplementary material of Kilteni et al. 2020), it was described that the apparatus from Kilteni et al. (2019) had the opportunity to apply the forces and online tune them based on a feedback controller. The first difference, regarding the subjective determination of forces, should not be considered as critical, since all subjects received the same force values (see our “Methods”). However, we think that the second difference between the setups, the re-binning of trials, might actually explain the stronger results in Kilteni et al. (2019) as this procedure might reduce noise and thereby lead to clearer results. Third, Kilteni et al. (2019) used the same auditory cue for both trial types here. However, the change of 5 exposure and 1 test trials was presented as in the original study. Accordingly, participants also expected a test trial in every sixth trial. Thus, there should be no difference with regard to expectation between our experiments and those of Kilteni et al. (2019). Furthermore, the delay between the first and second touch was randomized between 800 and 1500 ms (Kilteni et al. 2019). We chose a fixed interval of 1500 ms in our experiment, leading to a

better prediction of touch. Subjects have been able to reliably predict the occurrence of touch on their finger. Moreover, the authors from the original study (Kilteni et al. 2019) introduced a baseline as a no-movement condition. For the purpose of replication, the 0 ms and the 100 ms test delay were most interesting since in these, the significant differences were found in the original study. In addition, the test subjects' finger was not fully immobilized during the experiments, which could allow for minor perceptual changes and the applied forces not having the desired magnitude. Lastly, concerning the setup, subjects in the experiment by Kilteni et al. (2019) were asked to fixate a cross at a distance of 2 m during all conditions. The view of their hand and upper arm was impaired by a black screen. In our setup, the left forearm and hand were masked from participants as it was covered by the metal arch. In Experiment 3, we observed effects as reported by Kilteni et al. (2019). After an exposure delay of 0 ms, sensory attenuation was found at a test delay of 0 ms but not at 100 ms, whereas after an exposure delay of 100 ms, the reverse was true, tactile intensity appeared weaker at a 100 ms compared to the 0 ms test delay. A significant interaction effect confirmed the modulation of the test delays by the exposure delays, constant with a temporal recalibration of sensory attenuation. The described differences between our setups might explain why our result are not as strong as those of Kilteni et al. (2019) in Experiment 3. Why was sensory attenuation temporally specific in Experiment 3 and affected test delays rather broadly in the first two experiments? Differences in the experimental setup between Experiment 1, 2 and Experiment 3 concern the presentation of test delays (adaptive staircase vs. constant stimuli), the duration of the touch (270 ms vs. 100 ms) and the number of test delays in the experimental sessions (3 vs. 1). The presentation method of test delays is unlikely to explain the different results. Storch and Zimmermann (2022) showed a successful measurement of sensory attenuation for visual stimuli using the adaptive staircase procedure Best PEST. The duration of the touch being very long in Experiments 1 and 2 might be more likely to be responsible for a temporally broader effect of sensory attenuation. However, a recent study by Kilteni et al. (2023) used a touch duration of 250 ms and did find a difference between 0 and 100 ms test delays. It is hard to believe that the 20 ms difference to the test duration in our first two experiments should produce the different results. The major difference between Experiment 1, 2 and Experiment 3 is the number of test delays. Presenting only a single test delay as in Experiment 3 might allow temporal recalibration narrowly tuned to the singularly probed delay. In this view, a broader range of test delays might likewise lead to a broader tuning of the sensory attenuation time-course. Even though we blocked test delays in Experiment 2, the presentation of different delays in a single session might still have reduced temporal selectivity

of sensory attenuation. One possibility for the broad tuning of sensory attenuation might be that presenting several test delays decreases the ability to distinguish their durations. Regression to the average duration is a well-known effect occurring when different durations have to be judged (e.g., Zimmermann and Cicchini 2020). Our results showed no significant difference in sensory attenuation between the two delay conditions of 0 ms and 100 ms in Experiment 1 and 2. This finding led us to exclude the possibility of temporal recalibration effects in these experiments. The lack of differentiation in attenuation between the two delay conditions implies that participants' perception of the timing between their actions and the resulting sensory feedback remained relatively constant. In Experiment 3, we fixated subject's finger with tape and broadened the range of the subjectively perceived stimulus strength. We observed the well-known phenomenon of sensory attenuation between a test delay of 0 ms and 100 ms in this experiment. The necessity to fixate the finger of subjects suggests that sensory attenuation is highly susceptible for differences between the predicted and the actual force. It is one of the key statements of the first experiments that even small methodological changes might influence the observed effects of sensory attenuation.

The favorite theoretical approach to explain the phenomenon of sensory attenuation involves an internal forward model that predicts the sensory consequences of a button press (Blakemore et al. 2000, 2002). Based on a copy of the motor plan to press the button, the expected intensity of the ensuing tactile sensation and the time of its occurrence will be predicted. If the predicted and the actual sensation match, sensory attenuation will be observed. The content of the predictions is likely shaped by experience, given that signal transductions speeds and motor execution might change across the lifetime. Systematic mismatches between predicted and actual sensations lead to adaptation in many cases, likely to be processed within a forward model (Shadmehr et al. 2010). Recent literature findings also challenged the interpretation of the forward model (Press et al. 2020; Yon et al. 2018, 2021). In these studies, sensory consequences were amplified instead of weakened by the prediction of sensorimotor processes. Representations of visual brain areas changed towards expected action outcomes which makes the explanation of domain-general ideas more plausible (Yon et al. 2018). The authors hypothesize that an increased importance of prediction errors or sensory gating may be responsible for these attenuating effects. It is important to note that expectations can bias our actions towards perceiving expected outcomes, as highlighted by Yon et al. (2021). However, recent literature findings found evidence against this enhancement view for attenuation of self-touch (Job and Kilteni 2023; Kilteni and Ehrsson 2022).

Roussel et al. (2013) suggested a model based on the ideomotor theory, stating that the preparation of a motor movement consists in the preactivation of the sensory consequences of that movement. Brown et al. (2013) offer an explanation of sensory attenuation that reflects the active inference perspective of predictive coding. The theory holds that around the time of movements sensory processing prioritizes the proprioceptive consequences of these movements, thus leading to sensory attenuation in other sensory channels. This account is in agreement with findings of sensory attenuation for visual (Cardoso-Leite et al. 2010; Desantis et al. 2014; Hughes and Waszak 2011; Yon and Press 2017; but see Schwarz et al. 2018) and auditory stimuli (Baess et al. 2009; Weiss et al. 2011). In both models (Brown et al. 2013; Roussel et al. 2013), the time when sensory attenuation starts should be coupled to the onset of the movement since it is claimed that movement preparation factors are responsible for the effect. We have recently demonstrated that the tactile sensation felt in the active hand when pressing a button or a force sensory is necessary for sensory attenuation at the passive finger to occur (Fritz et al. 2022). We argued that attention shifting to the active finger to process the tactile sensation leads to reduced attentional resources in the passive finger, resulting in sensory attenuation. This idea, when applied to sensory attenuation of self-touch, cannot account for a temporal dissociation of the active touch by the subject and the time when sensory attenuation starts. Since the tactile sensation felt during the active touch is never shifted in time, sensory attenuation should also stick to the time of the movement. However, our explanation was proposed for sensory attenuation of external events like visual or auditory events. There are many arguments suggesting that sensory attenuation for external events and for self-touch rely on separate mechanisms (Dogge et al. 2019).

In conclusion, we show in three experiments that the temporal spread of sensory attenuation depends on the temporal range of test delays. We replicated the original report of temporal recalibration of sensory attenuation (Kilteni et al. 2019) in which a single test delay was used. With this experimental design, sensory attenuation was tightly tuned to the exposed delay. In experiments with three test delays presented in one session, we found a much broader tuning of sensory attenuation. Perceptual indistinguishability of the different test delays through regression to the mean might explain the broad temporal spread of sensory attenuation.

Author contributions EZ designed the research, CF performed the research, CF analyzed the data, and CF and EZ wrote the paper.

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Data availability The datasets generated and analyzed during the current study are available in the repository: <https://osf.io/thfrj/>.

Declarations

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

Ethics approval and consent to participate All experiments were in accordance with the Declaration of Helsinki.

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Tactile motor attention induces sensory attenuation for sounds

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ABSTRACT

Sensory events appear reduced in intensity when we actively produce them. Here, we investigated sensory attenuation in a virtual reality setup that allowed us to manipulate the time of tactile feedback when pressing a virtual button. We asked whether tactile motor attention might shift to the tactile location that makes contact with the button. In experiment one, we found that a tactile impulse was perceived as more intense when button pressing. In a second experiment, participants pushed a button and estimated the intensity of sounds. We found sensory attenuation for sounds only when tactile feedback was provided at the time the movement goal was reached. These data indicate that attentional prioritization for the tactile modality during a goal-directed hand movement might lead to a transient reduction in sensitivity in other modalities, resulting in sensory attenuation for sounds.

1. Introduction

A pivotal requirement for successful interaction with the environment is the ability to distinguish sensory stimuli that are produced by ourselves from those that have an external cause. The plethora of examples illustrating this need ranges through the animal kingdom from the electric fish that can dissociate self- and externally produced electric fields (Bell, 2001) to humans who are not disturbed by the retinal motion that is generated by their own eye movements (Wurtz, 2018). Research into these phenomena early on demonstrated that a signal must exist that tells sensory areas about upcoming movements (von Holst & Mittelstaedt, 1950). In consequence, sensory areas alter their receptivity for the sensory effects produced by that movement. The ensuing attenuation of sensory events has been found for tactile (Bays, Flanagan, & Wolpert, 2006), auditory (Weiss, Herwig, & Schütz-Bosbach, 2011) and visual events (Cardoso-Leite, Mamassian, Schütz-Bosbach, & Waszak, 2010). A comparator model account has been proposed in which the initiation of a movement triggers an efference copy that is used to build up a forward model that predicts the consequences of the movement (Blakemore, Wolpert, & Frith, 2002). If the prediction and the actual sensation match, the strength of that sensation is reduced, resulting in sensory attenuation.

Sensory attenuation has been previously tested for body-related events (Dogge, Custers, & Aarts, 2019). Predictions focused on action outcomes that are closely related to the direct actions itself. This model has been expanded to account for sensations that are not body-related (Dogge et al., 2019). Thus, explanations and effects of sensory attenuation for external events, like sounds generated by a button-press, must be distinguished from sensory attenuation for self-touch (Bays et al., 2006). Although both phenomena share common elements, evidence suggests that the two effects rely on separate neural mechanisms (Dogge et al., 2019). For instance, sensory attenuation of self-touch is spatially selective for the goal location of the touching movement (Bays, Wolpert, Haggard, Rosetti, & Kawato, 2008; Kiltner, Houborg, & Ehrsson, 2019; Knoetsch & Zimmermann, 2021). It can be predicted precisely because - unlike in

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most experiments on attenuation of external events - the position of the tactile sensation exactly matches the position of the touch. Furthermore, the connection between touch and tactile sensation is over-learned across the lifetime whereas the contingency between a movement (e.g. a button press) and an arbitrary external event must be trained to be predictable. However, for external events studies have shown that sensory attenuation occurs even if sounds merely coincide unpredictably with a button press (Bäå, Jacobsen, & Schröger, 2008; Horváth, Maess, Baess, & Tóth, 2012).

In our study we tested a novel hypothesis concerning sensory attenuation for sounds produced by closed-loop button presses. In closed-loop movements, feedback about the success of a movement is available and informs the actor to stop movement execution.

We assumed that pre-motor attention during these goal-directed hand movements improves tactile sensitivity at the predicted time when the hand will make contact with the desired object. Motor induced attention shifts are known to occur for several movements: For eye - (Deubel & Schneider, 1996) and for pointing (Baldauf, Wolf, & Deubel, 2006) movements, it has been repeatedly demonstrated that visual attention shifts to the goal location of the movement shortly before movement onset. The purpose of that shift is to predict the sensory consequences following movement termination in order to estimate movement success and - in the case of saccade eye movements - to establish visual stability across the movement (Baldauf & Deubel, 2008). A similar predictive attention shift has been found for pointing movements. Deubel and colleagues (1998) demonstrated that for the preparation of a pointing movement to a certain location, the perceptual processing is partially initiated even before movement onset. Similarly, to the attention effects observed at the time of saccades, discrimination performance presented close to the goal object of a pointing movement was higher than when presented at other locations.

Our data suggests that goal-directed movements like button presses induce tactile sensitivity to the moving hand in order to prioritize processing. In consequence, processing in other sensory modalities is decreased. The transfer of attentional resources between the tactile and the auditory modality is especially likely given their functional connectivity. The human somatosensory cortex co-activates with auditory cortex during the processing of vibrations and texture (Butler, Foxe, Fiebelkorn, Mercier, & Molholm, 2012; Iguchi, Hoshi, Nemoto, Taira, & Hashimoto, 2007; Nordmark, Pruszyński, & Johansson, 2012; Schürmann, Caetano, Hlushchuk, Jousmäki, & Hari, 2006). An influence of attention on these two cortical systems was already described by Gescheider, Sager, and Ruffolo (1975). When auditory and tactile stimuli were presented individually or simultaneously, the cognitive processing was only impaired for the concurrently occurring stimuli. Thus, the distribution of attention was an important determinant of performance. Also in recent studies, Convento and colleagues (2018) demonstrated that participants were impaired in an auditory frequency discrimination task when they received TMS stimulation over S1 and attended to tactile frequency information.

In this study we raised two major questions: First, is tactile sensitivity more increased at the time the hand makes contact with the button than at the beginning of the movement? It is long known that during arm-movements, tactile gating is responsible for increased tactile thresholds while the movement is ongoing (Chapman, Bushnell, Miron, Duncan, & Lund, 1987). Juravle, Deubel, Tan, and Spence (2010) tested tactile thresholds while participants had to grasp a computer mouse. They found that tactile sensitivity in the phase after the movement is significantly higher compared to the execution phase of the movement. The threshold values decrease from preparation to execution and increase again from execution to the phase after the movement (Juravle et al., 2010). We tested tactile thresholds during closed-loop button-press movements that are commonly used to measure sensory attenuation of external events (Weiss et al., 2011). Second, does attention processing the tactile sensation during a button press determine attenuation for sounds that are contingent on the button press?

We investigated these questions in a virtual reality setup that allowed us to manipulate the time of the tactile feedback when pressing a button. With our virtual reality setup, we could control the presence of tactile feedback. In studies investigating tactile gating and sensory attenuation an activation of the tactile modality is included, such as participants touching their own hand (Voudouris & Fiehler, 2017) or grasping an object (Juravle et al., 2010). These setups therefore include two tactile sensations, the feedback when touching the object in addition to the probe stimulus delivered by the experimenter. With the help of the virtual reality design, we were able to replace the physical feedback with artificial tactile feedback.

In our study a virtual button was presented in a head-mounted display and tactile feedback was provided via mini-vibrators that were attached to the participants' index fingers. In Experiment 1, we tested perceived vibration intensity at three different movement phases and in a baseline condition. In Experiment 2, we sought to find out whether the presence of tactile feedback determines sensory attenuation of actively produced sounds. In Experiment 3 we asked whether the putative interaction of tactile stimulus presentation and sensory attenuation for sounds is dependent on active movements.

2. General methods

2.1. Participants

A total of 30 study participants took part in Experiment 1 (including one author). For one participant psychometric functions could not be estimated, indicating that the task was not performed correctly. Therefore, the final sample in Experiment 1 consisted of 29 right-handed participants with unrestricted vision or vision correction (age: 18–56 years [$M_{\text{age}} = 26.52$, $SD = 9.87$], gender: 11 male, 17 female, 1 non-binary).

Moreover, we calculated a Baseline condition for Experiment 1 post-hoc. For this condition we used different participants. Here, 29 right-handed participants with unrestricted vision or vision correction (age: 18–52 years [$M_{\text{age}} = 24.46$, $SD = 9.14$], gender: 10 male, 19 female) were tested.

In Experiment 2, 25 right-handed participants with unrestricted vision or vision correction took part (age: 19–36 years [$M_{\text{age}} = 24.03$, $SD = 3.38$], gender: 6 male, 19 female).

Experiment 3 contained 20 right-handed participants with unrestricted vision or vision correction (age: 19–64 years [$M_{\text{age}} = 32.55$, $SD = 14.34$], gender: 9 male, 11 female).

Participants were recruited in the University Düsseldorf or via social networks. Experiments were approved by the local ethics committee of the Faculty of Mathematics and Natural Sciences of Heinrich Heine University, Düsseldorf (identification number: 757184), and are in accordance with the Declaration of Helsinki. Handedness was assessed using the Edinburgh Handedness Inventory and all participants were classified as right-handers. Participants were compensated with participation hours or remunerated by means of an expense allowance. Informed consent was obtained from all participants.

2.2. Power analysis

We conducted a power analysis post-hoc. Fraser and Fiehler (2018) introduced a similar study where participants were asked to do a pointing task with a vibration pad being taped to their index finger. They used a repeated measures ANOVA assessing the effects of time of stimulation (early and late) and the target size.

The interaction in the study of Fraser and Fiehler (2018) showed an effect size of $\eta_p^2 = 0.24$. With an alpha level of $\alpha = 0.05$, a Power of 0.8 and $\rho = 0.55$ for a repeated measures ANOVA with three measurements, a total sample size of $N = 27$ for Experiment 1 is required.

For a 2x2 repeated measures ANOVA in Experiment 2 a total sample size of $N = 23$ ($\eta_p^2 = 0.24$, $\alpha = 0.05$, Power = 0.8, $\rho = 0.55$) is required.

A paradigm very similar to ours was used by Gillmeister and Eimer (2007) to study the effects of touch on auditory processing. Since no effect sizes were added by authors, we adapted the number of subjects and also tested 20 subjects in Experiment 3.

As described below, our conclusions depend on many additional tests that are not included in this power analysis. Thus, the identified sample sizes should be considered a minimum for our study.

2.3. General materials

The Experiments took place in the same setting with only minimal adjustments. Participants in the experiments were asked to press a button in a virtual reality environment, which was presented to the participants through VR goggles (Oculus Rift Development Kit 2). The VR goggles included a horizontal and vertical field of view of 100° and a refresh rate of 60 Hz. In the head mounted display, participants saw a blue/green virtual button in front of a dark background. Hand movement of participants was captured with a motion sensor (Leap Motion, Orion V 2.3.1+31549 sampling at 60 Hz with a field of view of $140 \times 120^\circ$). A virtual hand model was shown that

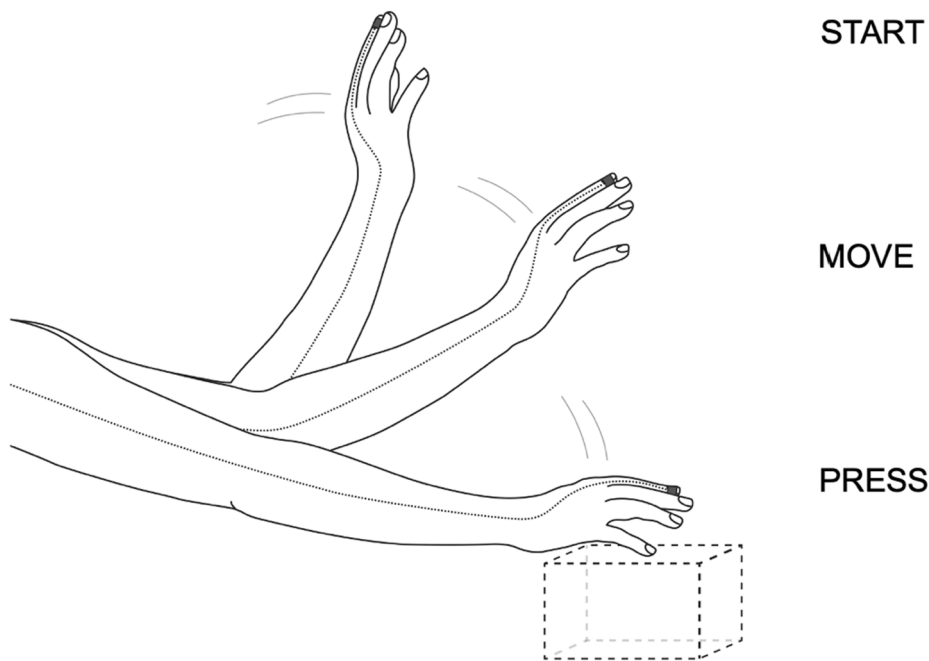


Fig. 1. Experimental setup. Participants were asked to perform a goal-directed hand movement to press a virtual button. During the movement the hand starts perpendicular to the button (Start), is then moved down towards the button (Move) and ends the movement with a button press (Press). The mini-vibrators attached to the right index finger are shown as black dots and their cables as grey lines. Participants experienced a tactile stimulation on the right moving index finger either during Start, Move or Press hand movement time (Experiment 1). A comparison stimulation was delivered 700 ms after the button press to the resting index finger of the left hand. The virtual button is presented with a dotted rectangular box..

moved synchronously with the real hand. Vibrotactile stimuli were presented via mini-vibrators that were attached to the right index fingers of the participants. The vibrotactile stimuli were controlled by an Arduino Nano microcontroller ATmega328 operating at 5 Volt. The experiments were run on a MacBook Pro (Retina, 15-inch, 2015).

3. Experiment 1

3.1. Procedure in Experiment 1

In Experiment 1, participants had to perform a goal-directed hand movement to press the virtual button with their right hand. In each trial they made an arm movement starting with the right hand and forearm held up and moved downwards to press the button (see Fig. 1). The virtual button went down 5° when pressed.

Each trial started with the presentation of a “Ready” message that was displayed on the left side of the screen center. After 500 ms, it was replaced by a “Set” message which was presented for 500 ms. Participant’s task was to press the button at the corresponding “Go” time, i.e. 500 ms after the appearance of the “Set” message. A vibrotactile stimulus was presented to the right index finger of the moving hand either before the start of the movement (Start), during the movement (Move) or when the button was pressed (Press). The first movement phase included all trials with tactile stimulations that occurred before the go-signal, the second movement phase included all trials in which tactile stimulation occurred equal to or after the go-signal and the third phase included all trials in which tactile stimulation occurred at the exact same time the button was pressed in virtual reality. These presentation times of the vibrotactile stimulus were randomized across trials, so the vibration could either occur during start, move or press phase. The vibration on the index finger of the right moving hand was constant in each trial (50% of the maximum vibration intensity of 5 Volt). After the button was pressed, a comparison vibration was delivered 700 ms later to the index finger of the resting left hand. The comparison vibration intensity varied randomly across trials between 20 and 40% and 60 80% of the maximum value of 5 Volt (in 6 equidistant steps). For a vibration intensity of 20%, 30% and 40% the vibromotor was driven with a voltage of 1,7 V, 2 V and 2,3 for 300 ms each. For a vibration intensity of 60%, 70% and 80% the motor was driven with 2.9 V, 3.2 V and 3.5 V. As the vibration was strongest with a control of 4.1 V and no longer perceptible under 1.1 V, we chose these values as the start and end points of vibration control. The movement phase as well as the vibration strength was chosen randomly. After each trial, participants had to decide which vibration was perceived stronger by using a foot pedal (UPC ECS-PPD-F) placed under the table. Pedal pressing was counterbalanced between participants with either pressing the right pedal when the first vibration felt stronger and the left pedal when the second vibration felt stronger or vice versa. Then, after giving an answer, the next trial started immediately. A total of 180 trials were conducted in the first session (60 trials for each of the three movement phases; ten trials for each vibration intensity of the comparison vibration per time point).

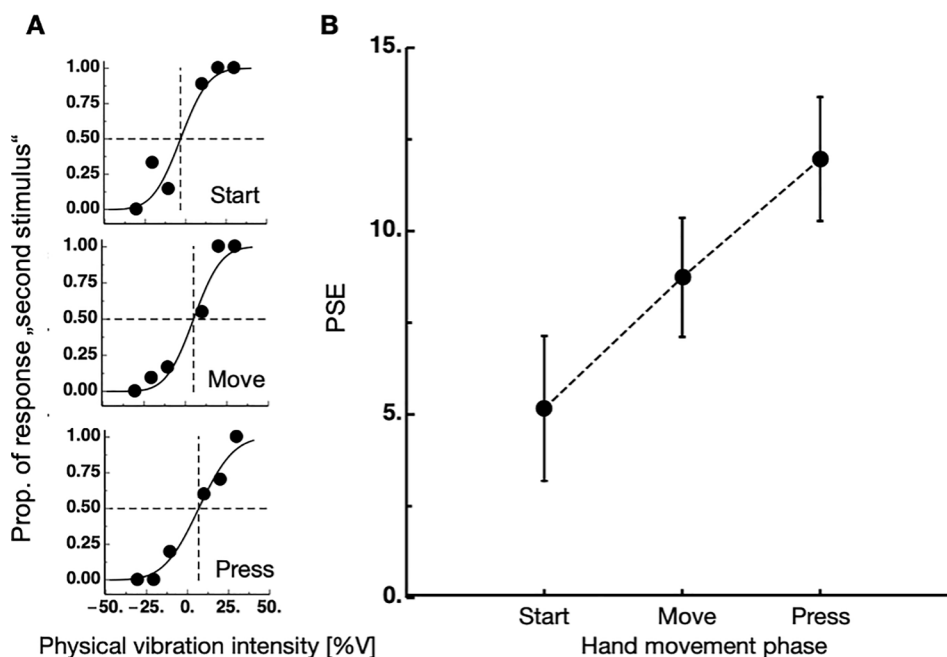


Fig. 2. Results of Experiment 1. (A) Psychometric functions of an example participant for the three movement phases. Proportions of second stimulus (corresponding to intensity at resting hand was stronger) are shown against physical vibration intensity. 50% of physical vibration intensity refers to a value of 0 here. (B) Average perceived vibration intensities for the three hand movement phases. The abscissa shows the deviation from the standard stimulus (positive numbers represent overestimation of vibration intensity). Error bars represent S.E.M. Black dotted line with greyish background shows the results for the Baseline condition.

In the Baseline Condition of Experiment 1 participants were required to keep their arm stationary. They were seated in front of a table with the VR goggles on and were asked to distinguish between the same stimuli levels presented in the movement conditions. Stimuli were presented with a temporal interval duration of 750 ms. The foot pedal was used to decide which vibration felt stronger.

3.2. Data analysis

For Experiment 1, we analyzed offline when the vibration occurred with regard to hand movement position. In total, we differentiated between three hand movement phases.

As stated, the first movement phase included all trials with tactile stimulations that occurred before the go-signal, the second phase included all trials in which tactile stimulation occurred equal to or after the go-signal and the third phase included all trials in which tactile stimulation occurred concurrently with the button press. On average, the number of trials per movement phase were distributed as followed: Start $M = 71.18$, $SD = 7.2$; Move $M = 51.38$, $SD = 4.74$ and Press $M = 65.54$, $SD = 4.02$. For all experiments, data were averaged for tactile/auditive intensities within each participant for each of the movement phases and Baseline. Afterwards all data were then fitted by a cumulative gaussian function. The point of subjective equality (PSE) represents the magnitude at which the probe vibration (tactile stimulation) is perceived as stronger than the comparison vibration/tone on fifty percent of the trials.

To identify whether there were significant differences between the PSEs and JNDs during the three movement phases in Experiment 1, a one-way repeated measures ANOVA was used. The data that supports the finding of the study are available at: <https://osf.io/edt74/>.

3.3. Results Experiment 1

In Experiment 1 a tactile stimulation on the right index finger was felt during one of the three hand movement phases: Start, Move and Press. Data for the three movement phases were fitted by cumulative gaussian functions individually for each participant. Psychometric functions of one exemplary participant are shown in Fig. 2. A one-way repeated measures ANOVA was conducted to identify whether the PSEs for the three hand movement phases differ significantly from each other ($M_{\text{Start}} = 5.16$, $SD = 10.64$, $M_{\text{Move}} = 8.73$, $SD = 8.73$; $M_{\text{Press}} = 11.96$, $SD = 9.09$). There was a statistically significant difference between all three movement phases ($F(2, 56) = 8.23$, $p = .002$, $\eta_p^2 = 0.227$). A post hoc analysis (tested against a Bonferroni-adjusted alpha level of 0.05/3) for the repeated measures ANOVA of PSEs revealed that there was a significant difference between the Start and Press movement phases ($MD = 6.80$, $SEM = 2.03$, 95% CI [2.63, 10.96], $p < .001$). No significance was found between Start and Move ($MD = 3.57$, $SEM = 1.56$, 95% CI [0.92, 7.37], $p = .113$) and between Move and Press ($MD = 3.27$, $SEM = 1.37$, 95% CI [-0.56, 7.715], $p = .179$).

Moreover, we compared all three conditions to the Baseline ($M_{\text{Baseline}} = 51.15$, $SD = 4.92$) with Bonferroni corrected paired t-tests ($\alpha = 0.05/3$). We found no significant effects between Baseline and the Start phase ($t(56) = 1.843$, $p = 0.071$). We found significant effects between Baseline and Move ($t(56) = 4.077$, $p < .001$, $d = 1.071$) as well as Baseline and Press ($t(56) = 5.632$, $p < .001$, $d = 1.479$).

We also analyzed JNDs with a one-way repeated measures ANOVA ($M_{\text{Start}} = 18.27$, $SD = 17.88$; $M_{\text{Move}} = 12.89$, $SD = 16.45$; $M_{\text{Press}} = 16.23$, $SD = 17.36$). No significant main effect for this ANOVA was found here ($F(2, 56) = 1.757$, $p = .182$, $\eta_p^2 = 0.059$).

4. Experiment 2

4.1. Procedure in Experiment 2

Experiment 2 was divided into two conditions, called 'no-tactile' and 'tactile'. It was randomized whether participants first started with the 'no-tactile' or 'tactile' condition. Both experimental conditions were conducted in the same virtual reality setup as Experiment 1. Again, participants were asked to perform a goal-directed movement to press the virtual button with the right hand within VR.

In the 'no-tactile' condition, a reference tone (MacBook sound 'Funk') was presented either during the start of the movement or when pressing the button. As the generation of a tone when button pressing seems quite natural, we assumed that participants perceived the tone as self-generated when pressing the virtual button. We only initiated a second movement time here (during start of the movement). We reasoned that for start as well as move phase no effects of sensory attenuation are to be found.

The tone was presented with 62.3 dB (50% of maximum intensity of the MacBook) through headphones. 700 ms after finishing the goal-directed movement, a probe tone was played, either with 80–60% or 40–20% of the maximal auditive intensity (67.2, 65.1, 63.6, 58.6, 55.1 or 58.6 dB). We based the individual sound volumes on the MacBook's loudness gradations. We then evaluated the associated decibel values using a decibel meter. Participants were asked to estimate which tone (reference vs. probe) was louder by pressing either the right or left button of the foot pedal placed on the floor. It was randomized between participants whether the first or second tone was assigned to the right side of the foot pedal. The timing of the reference tone (Start vs. Press movement time) as well as the volume of the probe tone (80–60% or 40–20%) was randomized. A total of 120 trials was conducted in the condition 'no-tactile' (60 trials for each of the two movement phases; ten trials for each auditory intensity per time point).

In the condition 'tactile' of Experiment 2 the main part of the test procedure remained similar to the condition 'no-tactile'. Each trial started 500 ms after a "Set" message and a probe tone was played either before or after the goal-directed movement. However, a mini-vibrator was attached to the participant's right index finger. Each time the button was pressed within VR, participants felt a vibration on the right index finger of their moving hand. More precisely, in 100% of trials in condition 'tactile' a stimulus was delivered to the

right moving index finger during the button press. In 50% of trials a tone was played when starting the movement and in 50% of trials the probe tone was played when pressing the button. Headphones prevented auditory perception of the vibration sound.

A total of 120 trials was conducted in the condition 'tactile' (60 trials for each of the two movement phases; ten trials each for each auditory intensity per time point). Presentation time of the stimulus and auditory intensity were randomized across trials.

For experiment 2 we used a 2×2 factorial design to perform an ANOVA for repeated measures to find significant differences between the PSEs and JNDs of 'no-tactile' and 'tactile'.

4.2. Results Experiment 2

In half of the trials in Experiment 2 a tone was played when subjects pressed the button and in the other half the tone was played when they started the movement. Additionally, in the condition 'tactile', a tactile stimulation was felt on the moving index finger when subjects pressed the button. In the other condition 'no-tactile', a tactile stimulation was not felt. A 2×2 repeated measures ANOVA with tactile stimulation ('tactile' vs. 'no-tactile') and hand movement time (Start vs. Press) as factors and the PSEs of the perceived auditory intensities as the dependent variable was conducted ('tactile': $M_{\text{Start}} = -0.81$, $SD = 9.04$; $M_{\text{Press}} = -7.58$, $SD = 12.37$; 'no-tactile': $M_{\text{Start}} = -1.81$, $SD = 12.31$; $M_{\text{Press}} = -2.84$, $SD = 10.32$). The two main effects for tactile stimulation ($F(1, 24) = 1.302$, $p = .265$, $\eta_p^2 = 0.051$) as well as hand movement time ($F(1, 24) = 3.839$, $p = .062$, $\eta_p^2 = 0.138$) showed no significance (see Fig. 3). The interaction between the hand movement time * stimulation showed a significant difference ($F(1, 24) = 4.71$, $p = .04$, $\eta_p^2 = 0.164$). A post hoc analysis (tested against a Bonferroni-adjusted alpha level of $0.05/2$) revealed that this significance is to be found between the condition of Start and Press in the tactile condition ($MD = 6.77$, $SEM = 2.39$, 95% CI $[0.148, 13.39]$, $p = .021$). No significance was found between the other conditions ($p > .176$).

We also analyzed JNDs with a repeated measures 2×2 ANOVA with tactile stimulation ('tactile' vs. 'no-tactile') and hand movement time (start vs. press) as factors ('tactile': $M_{\text{Start}} = 28.02$, $SD = 30.9$; $M_{\text{Press}} = 22.35$, $SD = 20.18$; 'no-tactile': $M_{\text{Start}} = 19.08$, $SD = 12.39$; $M_{\text{Press}} = 15.71$, $SD = 13.51$, $\eta_p^2 = 0.227$). The main effect of hand movement time ($F(1, 24) = 1.519$, $p = .230$, $\eta_p^2 = 0.060$) was not significant. However, there was a main effect for the tactile stimulation ($F(1, 24) = 6.24$, $p = .020$, $\eta_p^2 = 0.206$). No significant interaction was found ($F(1, 24) = 192$, $p = .665$, $\eta_p^2 = 0.008$).

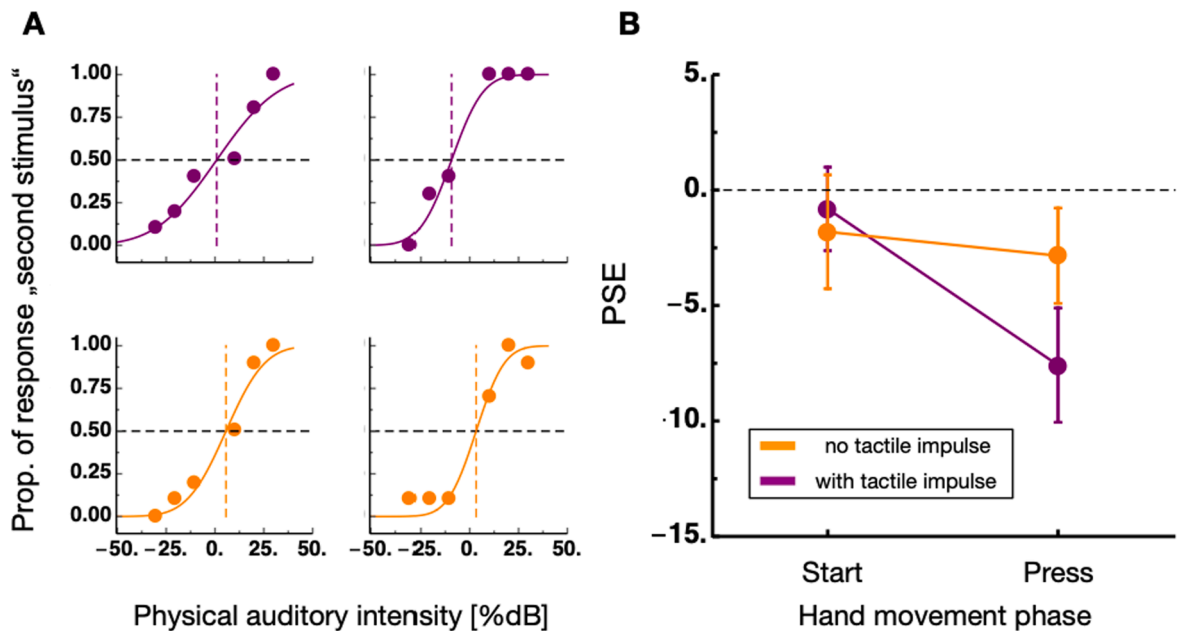


Fig. 3. Results of Experiment 2. (A) Psychometric functions of an example participant for the two conditions. Proportions of response for second stimulus are shown against physical auditory intensity. (B) Average perceived sound intensities from session with (shown in purple) and without (shown in orange) tactile stimulation for sounds presented at the Start and the Press time of the movement. The abscissa shows the deviation from the standard stimulus (positive numbers represent overestimation of auditory intensity). Error bars represent S.E.M. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

5. Experiment 3

5.1. Procedure in Experiment 3

To identify whether the putative interaction of tactile stimulus presentation and sensory attenuation for sounds is dependent on the active movement, participants did not perform the button pressing movement during Experiment 3. Participants were placed in front of a table with headphones on and were told to keep their hands rested on the table without any movement. During the test phase they heard two different tones via headphones. The first tone was played with 50% of the maximum auditory intensity of the MacBook Pro. The second tone, as a comparison tone, was presented 700 ms later with either 80%, 70%, 60% or 40%, 30%, 20% of the maximum auditory intensity. After each trial participants had to decide which tone was perceived louder by using a foot pedal placed under the table. Participants had to press the right button of the foot pedal, when the first tone was perceived as louder or the left pedal when the second tone was perceived as louder (or vice versa). After entering the answer, the next trial started immediately. In the first condition, no tactile stimulation was presented during the discrimination task ('no-tactile'). In the second condition ('tactile'), a mini-vibrator was attached to the participants right index finger. A vibration with 70% of maximum intensity was felt on the index finger paired with the first tone. The order of 'tactile' vs. 'no-tactile' was randomized between participants.

5.2. Results in Experiment 3

To analyze data in Experiment 3 a *t*-test for repeated measures was used. Data was divided into 'tactile' (a tactile stimulation was felt during the sound discrimination) and 'no-tactile' (absence of tactile stimulation during sound discrimination). A *t*-test for repeated measures revealed no significant differences in the PSEs for the condition of 'tactile' ($M = 53.895$, $SD = 7.555$) and 'no-tactile' ($M = 51.15$, $SD = 6.93$): $t(19) = 1.3$, 95% CI $[-1.67, 7.16]$, $p = .208$. Also a repeated measures *t*-test for JNDs showed no significant effects for the difference between 'tactile' ($M = 14.03$, $SD = 8.84$) and 'no-tactile' ($M = 14.55$, $SD = 9.38$): $t(19) = -0.188$, 95% CI $[-6.31, 5.27]$, $p = .853$. The results for Experiment 3 are presented in Fig. 4.

6. Discussion

In this study we investigated the underlying processes that could be responsible for sensory attenuation of self-generated sounds during closed-loop movements. In Experiment 1 we asked if in goal-directed button pressing movements, tactile sensitivity is increased at the time the hand makes contact with the button. We found that apparent tactile stimulus intensity was higher at the time when the hand reached the movement goal than before or during the movement. This finding indicates that tactile attention increases at the time when the hand reaches the goal object and transiently improves tactile sensitivity. Moreover, we introduced a no-movement Baseline condition here which showed significantly lower PSE values than the Move and Press condition. This rules out that effects could be driven by the presentation time of stimuli, as the first stimulus appeared earlier in relation to the second stimulus in the Start and Move

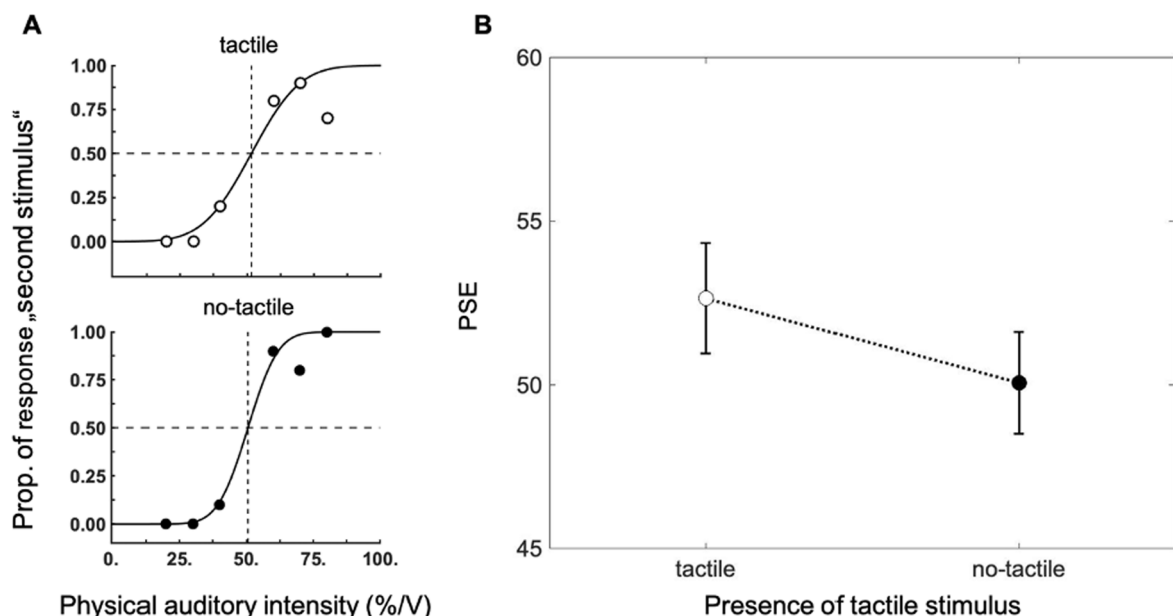


Fig. 4. Results of Experiment 3. (A) Psychometric functions of an example participant for the two conditions. Proportions of response to the second stimulus are shown against physical auditory intensity. (B) Average perceived sound intensities from session with and without tactile stimulation. Error bars represent S.E.M.

phases compared to the button press.

Previous studies found a reduction of tactile sensitivity during arm movements, a phenomenon known as gating (Chapman et al., 1987). The phenomenon has been described frequently for reaching and grasping movements (Colino & Binsted, 2016; Colino, Lee, & Binsted, 2017). Tactile gating demonstrates that tactile stimuli on the hand are harder to detect during movement (Buckingham, Carey, Colino, deGrosbois, & Binsted, 2010; Colino et al., 2017). Usually, this phenomenon starts shortly before movement initiation and builds up again towards the movement goal (Juravle et al., 2010) and tactile sensitivity in the phase after the movement is significantly higher compared to the execution phase of the movement (Voudouris & Fiehler, 2021). Suppression for probed body parts that did not make contact with the goal object is significantly higher (Colino, Buckingham, Cheng, van Donkelaar, & Binsted, 2014). Suppression of tactile information is clearly driven by task-relevance. As Manzone, Inglis, Franks, and Chua (2018) showed, suppression during movement varied with task relevance so that targeted movements showed less suppression (Manzone et al., 2018, Colino et al. (2014)). In our study, we provide tactile feedback directly to the pressing finger making the tactile stimulation essential to end the closed-loop button press. Thus, task-relevancy of the tactile feedback in our study is maximized, explaining the absence of suppression. As we conducted our study in a virtual reality setup, no other tactile sensation could confound effects. In other studies, such as Juravle et al. (2010) or Voudouris and Fiehler (2017) this confounding was less controlled. In the study of Juravle et al. (2010), participants moved their hand from a computer mouse (start position) to a goal mouse (goal position) at the end of the table. They found that tactile thresholds increased in the moment the hand picked up the object. Though, tactile thresholds were measured while the finger made physical contact with the object. The sensation of pressure might have reduced the apparent intensity of the tactile impulse.

In Experiment 2 we wondered whether the boost of tactile sensitivity we observed in Experiment 1 would lead to sensory attenuation for sounds. Participants judged the intensity of sounds in two conditions: Virtual button presses were either accompanied by a tactile stimulation or not. As stated above, for saccades, Deubel and Schneider showed (1996) that at the time of saccade onset, attention is bound to the target position. However, a recent study showed that attentional shifts preceding saccades that are executed to an extinguished target allow attention to spread (Szinte, Puntiroli, & Deubel, 2019). Thus, in the absence of the visual target, attention is no longer bound to the goal location of the saccade. Following this analogy, we assumed that only in the presence of tactile stimulation, attention would be bound to the tactile modality. Indeed, we found sensory attenuation for sounds only when virtual button presses produced a tactile stimulation.

In principle, this interaction could also occur without the movement. However, sensory attenuation of sounds has been shown to occur only for active movements (Timm, SanMiguel, Keil, Schröger, & Schönwiesner, 2014). In Experiment 3 we tested auditory perception in the presence and absence of tactile stimuli without movements. Here we found no significant differences, supporting the effects of Timm and colleagues (2014) that the hand movement was a prerequisite for the given effects of attentional shift.

The occurrence of sensory attenuation in the auditory domain is consistent with current literature findings (Mifsud & Whitford, 2017; Timm et al., 2014). However, we believe that the boost of tactile sensitivity observed in Experiment 1 could be an indicator for sensory attenuation in Experiment 2. We theorize that the reaching of the movement goal, e.g., touching the button, is prioritized in the moment of button pressing. Therefore, attention is bound to the touching finger at this exact moment. In line with our theory, in the condition in which no tactile stimulus was presented and no attentional resources were required for its processing, sensory attenuation was virtually absent. Attention shifts are known to amplify neural responses and perceived intensity (Desimone & Duncan, 1995; Posner & Dehaene, 1994; Posner & Petersen, 1990), thus explaining the increase in tactile and the decrease in auditory sensitivity. Why would attentional prioritization of the tactile modality create an imbalance between the tactile and the auditory modalities? This linkage might be explained by the close neural connectivity of both modalities. Coactivation of the somatosensory and the auditory cortex have been reported previously (Butler et al., 2012; Convento, Rahman, & Yau, 2018; Iguchi et al., 2007; Nordmark et al., 2012; Schürmann et al., 2006) and an influence of attention on these two cortical systems was already described by Gescheider and colleagues (1975).

On the one hand, a putative limitation of our study might consist in the combination of the virtual button and the presentation of the tactile impulse, which subjects did not experience before participating in the experiment. On the other hand, with this setup we could successfully replicate the sensory attenuation effect. The idea that a sensorimotor contingency between the button press and the ensuing sensory effect must be established before the start of the experiment is based on a theoretical assumption about sensory attenuation that might be incorrect. Three EEG studies found that prediction of sensory consequences is not necessary for sensory attenuation of sounds to occur. When self- and externally generated stimuli were presented within the same experimental block, Baess, Horváth, Jacobsen, and Schröger (2011) found that N1 suppression for self-generated stimuli was even stronger. Furthermore, a study also showed that sensory attenuation occurs when stimuli are not predictable but merely coincide with a button press (Horváth et al., 2012; Lange, 2011). In Experiment 2, we showed that in the absence of tactile stimulation, no attenuation was observed. In itself the visual observation of the hand pressing the button has no influence on the reduced sensory intensity of sounds. A visual-tactile interaction might influence the observed effect. The most plausible reason why this should occur is that the visual hand motion allows to predict the time when the tactile stimulus will be applied.

7. Conclusion

In conclusion, we found sensory attenuation for sounds when tactile feedback was provided during a button-press movement but not when there was an absence of tactile stimulation. Our data suggest that during goal-directed hand movements attention transiently boosts tactile sensitivity at the time the hand reaches the goal object. This increase might be responsible for an imbalance between the tactile and the auditory domain, leading to reduced attentional resources in the latter and thereby to sensory attenuation for sounds.

CRediT authorship contribution statement

Clara Fritz: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **Mayra Flick:** Data curation, Methodology, Project administration, Resources, Validation, Visualization, Writing – original draft, Writing – review & editing. **Eckart Zimmermann:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author Contributions statement

EZ developed the study concept. All authors contributed to the study design. Testing and data collection were performed by CF and MF. CF performed the data analysis and interpretation under the supervision of EZ. All authors contributed to writing the several drafts of the paper and approved the final version of the manuscript for submission.

Data statement

The data of the study are available at <https://osf.io/edt74/>.

Author Note

An earlier version of this manuscript was published as a bioRxiv-preprint, available at <https://www.biorxiv.org/content/10.1101/2021.07.08.451581v1>.

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