Sensorimotor recalibration reverses the temporal constraints of somatosensory attenuation

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Abstract

Theories of sensorimotor control and learning state that our brain uses internal forward models to obtain efficient online motor control. A forward model uses the copy of a motor command to form a prediction of the movement's sensory consequence; if the prediction matches the sensory feedback, it is experienced attenuated. These predictions have shown to be temporally precise and short time delays between a movement and its expected consequence have demonstrated to reduce attenuation. However, since multisensory feedback is subject to many different and changing delays, it requires a flexible mechanism to calibrate perception of timing. This thesis investigates if the brain can learn to predict a new temporal relationship between action and sensory feedback and whether it reflects updating of an internal forward model.

120 participants across four experiments did a two-alternative forced choice task, where they triggered a 2 N tap delivered on their left index finger by tapping a sensor with their right index finger. The triggered tap was delivered immediately or with a delay in either exposure trials, response trials, or during both. During response trials, a second tap between 1 to 3 N was applied, and participants had to indicate if the self-triggered tap or the external tap was stronger. Before the force discrimination task subjects received either 50, 200, or 500 trials of initial exposure in a quick training session.

Our results show that after being exposed to a delay subjects' no longer attenuate immediate touch. However, only after 200 or more trials of exposure do subjects' show attenuation of the sensory feedback of 100 ms delayed touch. Attenuation of delayed touch seemed to increase with exposure. Importantly the opposite shifts in attenuation of immediate touch and delayed touch was correlated.

We conclude that these shifts in attenuation reflect recalibration of the predicted temporal relationship between action and consequence in an internal forward model. These findings are discussed in the context of sensorimotor learning and cerebellar processing.

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Introduction

Being able to quickly distinguish between what is the self and what is external is critical to human function. Likewise, determining whether what happens in the world is a result of our own actions or a result of an external cause is equally important. However, this poses several problems: First, there is such a vast amount of sensory information available to the brain, that processing all seems like an insurmountable task. Second, in order to have a unified and meaningful perceptual experience the brain must successfully integrate sensory information of several modalities. And third, sensory information of different modalities has different physical properties, are transduced, transmitted, and processed at different and, more importantly, constantly altering rates, yet we experience multisensory events at simultaneous.

Determining the temporal order of events in the world and adjusting our actions accordingly is vital to human survival. Quickly determining if a touch on our body is caused by our own action or a bug crawling, gives us the ability to quickly identify and remove the bug. Equally, if you hear a twig snap while walking in the forest quickly determining if it happened before or after your step quickly informs you whether the sound was caused by a predator or you and you can act accordingly. However, we face yet another problem when we have to act: Because of differing and slow transmission times of afferent sensory signals the motor system cannot rely on these for efficient online motor control (Wolpert, Miall, & Kawato, 1998, p. 338; Franklin & Wolpert, 2011, p. 425f). Additionally, there are delays on efferent signals to muscles and a delay to which they generate force which can also alter with time (ibid). This means that there are numerous circumstances which can alter the temporal relationship between motor commands and the resulting sensory consequences (events such as increasing in mass, muscle fatigue, tool-use, etc.).

This thesis will argue that in order to overcome these problems of temporal ambiguity and efficient motor control the brain predicts the sensory consequences from the motor command we execute and adjusts these predictions based on the sensory information it receives.

Temporal Recalibration

There are many artifacts and illusions that arise as a result of temporal processing and multisensory integration (Eagleman, 2008). For example, when subjects are shown a repeated series of the same stimuli they will perceive the time duration of the first presentation of the stimuli as longer (Rose & Summers, 1995). Similarly, if an oddball stimulus is displayed, during such a repeated presentation of similar stimuli, the perceived duration of the oddball stimulus will be significantly longer (Tse, Intriligator, Rivest, & Cavanagh, 2004). It is theorized that this phenomenon is correlated with repetition suppression and is a result of predictability between stimulus (Eagleman, 2008, p. 133). This phenomenon happens equally whether participants are presented a series of the number 1, or a series counting from 1 and up (i.e. 1-2-3-4-5 etc.) (Pariyadath & Eagleman, 2007; Eagleman 2008, p. 133). A similar suppression of cortical activity has been observed when the stimulus is a result of self-initiated motor act (Schafer & Marcus, 1973). This could further suggest a link between predictive mechanisms related to the outcomes of our actions and perceived timing of onset and duration of a stimuli.

Haggard and colleagues (2002) found that when we perform an action the perceived timing of the action and the perceived timing of the resulting sensory consequence is experienced being closer to each other than they are. The action is experienced happening slightly later than when actually performed and the result is experienced to happen earlier (ibid. p. 383). This intriguing phenomenon is termed ‘intentional binding’ and is theorized to be a compression in perceived time as a result of multisensory binding of our intentional action and its result. However, Stetson and colleagues (2006) presented an alternative explanation for this phenomenon. Because of the many temporal latencies related to multimodal sensory processing, correctly judging temporal order can be confounded by these changing delays (ibid). When integrating multisensory information our perception is drawn towards the slowest travelling signal in order to maintain a coherent experience (Vroomen & Keetels, 2010). Thus, they propose a single mechanism within the central nervous system that calibrates the temporal expectations between action and sensory consequence in order to correctly determine cause and effect (Stetson, Cui, Montague, & Eagleman, 2006). If this is the case then it should predict a novel illusion: When participants are exposed to a consistent delay between their action and the sensory consequence this mechanism will recalibrate temporal expectations and shift perception towards the delayed consequence. When the delay gets removed after exposure and feedback is immediate subjects will experience this feedback as happening before their action (ibid.).

They tested this using a psychophysical approach where participants had to perform a forced choice discrimination task. In their primary behavioural experiment participants triggered a flash on a screen by pressing a button. In 60% of the trials participants viewed either an immediate (35 ms intrinsic delay) or a 100 ms delayed (135 ms with intrinsic delay) flash on the screen. In the other 40% of trials the flash appeared anywhere between 150 ms before or after their press. In every trial participants had to make a forced choice between what occurred first: Their press of the button or the flash on the screen (ibid). They found a significant difference in the Point of Subjective Simultaneity (PSS: The point where participants experience their action and the consequence happening simultaneously) between the delay and no delay condition.

This shift in perception of simultaneity also occurs during cross-modal asynchronies (Fujisaki, Shimojo, Kashino, & Nishida, 2004; Vroomen, Keetels, de Gelder, & Bertelson, 2004). This cross-modal recalibration has been extensively researched and they all lead to a similar shift pattern across all cross-modal pairings suggesting that a single supra-modal mechanism is responsible (Hanson et al., 2008; Fujisaki & Nishida, 2009; Kuling et al., 2012; Ley et al., 2009; Machulla et al., 2016; Heron, Hanson & Whitaker, 2009). Stetson and colleagues (2006) however demonstrate in a control experiment that the shifts in PSS caused by cross-modal sensory asynchrony are less than half of motor-sensory shifts. Suggesting we adjust expectations and prediction through interaction and active engagement with the world (ibid). In a MEG study done recently, it was found that during lag adaptation visually evoked currents shift earlier and motor readiness currents shift later in a manner similar to the effects observed in intentional binding (Cai, Ogawa, Kochiyama, Tanaka, & Imamizu, 2018, p. 659f). The authors argue that the since the shift in readiness potential happened prior to sensory feedback it must be a result of prospective and predictive motor processing (ibid). Further, they argue that this prospective processing predictively modulates the shift in visually evoked currents (ibid).

Sensory Attenuation and the Internal Forward Model

A possible target mechanism or the module responsible for temporal recalibration is the internal forward model which is critical for successful online motor control. Predictive control of our motor actions is an important tool for motor control. Because multisensory feedback is subjected to noise and delays the motor system has to rely on predicted outcomes of an action (Wolpert et al, 2011, p. 740). This requires a model which can effectively simulate our actions and the environment (ibid). The basic idea of the forward model is that it uses the information of our executed action (The efference copy of the motor command) to predict the resulting sensory feedback (corollary discharge) of the action (von Holst, 1954; Sperry, 1950; Blakemore, Frith, & Wolpert, 1999a). When the prediction and the actual sensory feedback matches, the experienced feedback is then attenuated (Blakemore et al., 1999a). This mechanism provides perceptual stability during movement and also lets us quickly distinguish the self from the environment (Blakemore, Wolpert, & Frith, 2000, p. 11f). This is the explanation for why we can’t tickle ourselves. The tickling caused by our own movement is attenuated in the presence of the efference copy, however, when the sensation is externally generated the forward model lacks the necessary information to sufficiently predict and attenuate the sensation (Blakemore et al, 1999a). This process of continually predicting the congruency between the flow of actions and resulting consequences is essential to providing a sense of agency and confirming the causes of our actions (Jeannerod, 2006, p. 74). It is theorized that an implicit feeling of agency associated with our actions is derived from this same comparison process (Synofzik, Vosgerau & Newen, 2008, p. 222). It also confirms whether we successfully reached the intended goal of an action (Jeannerod, 2006, p. 20).

An important feature of the internal forward model is its’ ability to simulate a given movement and the predicted result of the movement without actually executing it (ibid, p. 21). Many studies have pointed towards that overt (executed actions) and covert actions (imagined movements which are not executed) are functionally equivalent. For example, when imagining executing a motor task, like walking a certain distance, it takes the same time to complete as the actual execution (Decety, Jeannerod, & Prablanc, 1989). Similarly, motor imagery follows Fitts law; The time duration of a movement increases with accuracy required (Georgopoulos & Massey, 1987; Decety & Jeannerod, 1996). The forward model has also been shown to predict sensory consequences “resulting” from an imagined movement over an actually executed movement (Kilteni, Andersson, Houborg, & Ehrsson, 2018). This suggests, that a movement is not necessary for sensory attenuation to occur, the imagined movement generates an efference copy from which sensory consequences can be predicted (ibid).

Figure 1. Sensory attenuation.

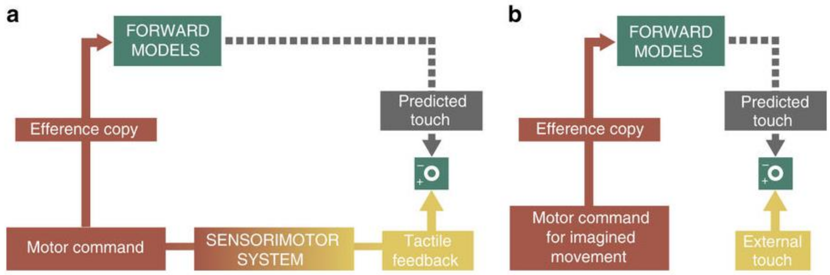

Figure 1. A computational model of imagined and executed movements. Sensory attenuation of self-generated sensations is a result of internal forward models which predicts sensory feedback given a copy of the motor command (**a**). When an externally applied touch lines up with the imagined self-tap of subjects during the experiment the external touch is attenuated similarly to if the touch was self-generated (**b**). (Figure taken from Kilteni, Andersson, Houborg & Ehrsson, 2018, p. 6).

Shergill and colleagues (2003) did a force matching task where participants were presented a force on their left index finger and then had to reproduce the force by either pressing with their right finger or controlling a slider. They found that when reproducing the force by pressing participants consistently underestimate the force they produced (Shergill, Bays, Frith, & Wolpert, 2003). However, when using the controller participants accurately reproduced the presented force (ibid). Using the inverse logic, pressing on top of the sensor during force presentation the externally generated force is attenuated and participants overestimate when reproducing the force controlling the motor with a slider (Kilteni et al, 2018). Congruency between the movement and the resulting consequence is key, when subjects’ movements are exposed to spatial perturbation the result is no longer attenuated (Blakemore et al., 1999a, p. 554). Similarly, using a two-alternative forced choice task to measure the point of equivalency between self-caused touch and external touch, touch was attenuated less the larger the delay between the movement and the resulting touch (Bays, Wolpert, & Flanagan, 2005, p. 1127). When delay between the movement and predicted sensory consequence reaches 300 ms and above it is no longer attenuated (ibid). Similarly, it was observed in temporal recalibration papers that the shift in perception decreased with increasing delay (Heron et al., 2009; Stetson et al., 2006). They argue as the delay between action and consequence becomes larger it is increasingly difficult to interpret the sensory result as self-caused (ibid.). Exactly at which point of delay this decrease in shift arises is still ambiguous. This is compatible with predictions of the internal forward also serving as a basis for associated feelings of agency over actions and their resulting sensory consequences (Synofzik et al, 2008, p. 222).

In a follow-up study using a similar approach Bays and colleagues (2006) confirming that the attenuation observed was caused by a predictive and not a postdictive process. Making subjects trigger a tap on their left index finger by pressing a sensor with their right index finger, they infrequently remove the sensor in random trials (Bays, Flanagan, & Wolpert, 2006). Regardless if the right index finger made contact with the sensor, the resulting tap on their left finger was attenuated (ibid). This reflects a predictive mechanism which attenuates self-generated sensory events on the grounds of planned motor activity (ibid).

There are many circumstances which change the relationship between our movements and the associated sensory consequences. Gradual and slow changes to our body through aging and development (bones growing, changes in muscle mass) coupled with more short-term factors like muscle fatigue alters the properties of the neuromuscular system (Franklin & Wolpert, 2011, p. 435). Additionally, we constantly learn new movements and discover new relationships between our action and the related sensory results when we engage in different tasks. Under these constantly changing conditions it is necessary to continually update internal models to keep them tuned to body status as well as the context of the external environment in order to accurately predict sensory feedback (ibid; Wolpert & Kawato, 1998). In order to have a wide repertoire of different motor behaviours with many different objects in a variety of differing contexts and environment it is theorized that sensorimotor control is a modular system (Wolpert & Kawato, 1998). The system is composed of several pairs of inverse and forward models. The inverse model acts as a controller providing the motor command required by the forward model to predict a future state (ibid, p. 1318). The benefit of a modular system comprising several pairs of inverse/forward model is that it explains how we can transfer from one learning context to another while retaining previously learned behaviours and without the newly learned motor behaviour interfering (ibid). It also gives an added explanation of how learning in one context can transfer to motor behaviour in another by combining the output of several model pairs (ibid, p. 1319).

Because there is, as previously established, a wide range of uncertainty and noise in sensory feedback, the prediction of the forward model is based on Bayesian inference (Körding & Wolpert, 2004; Körding & Wolpert, 2006; Wolpert et al, 2011, p. 740). In order to provide an accurate estimate of action outcomes a forward model predicts the outcome most likely to happen. This estimation is based on our prior statistical knowledge of the world combined with incoming sensory feedback to determine the probability of the next action outcome (ibid.). Combined with inverse models, which provide the efference copy, forward models use Bayesian inference to continually make and adjust estimations about our motor actions and their results in the world (ibid).

A good example of how internal forward models calibrate is tool-use. Effective use of tools is vital to success of the human species, they allow us to fulfil tasks otherwise impossible or much more efficiently than without tool use. When we use tools, several studies suggest they become an extension of our peripersonal body-space when we use them (Berti & Frassinetti, 2000; Farné & làdavas, 2000).

Kilteni and Ehrsson (2017a) showcase that sensory attenuation occurs when participants do the force-matching task by reproducing the presented force with a tool. Participants underestimated their produced force pressing with a tool similar to when they press with their finger (ibid.). Suggesting that the sensory predictions of a forward model also extend their predictions of sensory consequences caused by our actions with a hand-held tool (ibid., p. 6f). Interestingly, keeping in mind that tools extend our bodies, Kilteni & Ehrsson (2017b) found that the sensory predictions made by a forward model depend on the sense of ownership of the body. Using the Rubber Hand

Illusion (Botvinick & Cohen, 1998) to manipulate subjects' sense of body ownership, participants embodied a 3D printed hand equipped with a servomotor to make movements congruent with the subject's movements (Kilteni & Ehrsson, 2017b). They then performed the regular force-matching task (Shergill et al, 2003) in four different conditions across two experiments. The study found that participants attenuated touch during ownership of the fake rubber hand (Kilteni & Ehrsson, 2017b). Critically they also found, during ownership of the fake rubber hand, that ownership was negatively correlated with attenuation when the rubber hand was placed at a distance from the sensor, but the two real hands were aligned (Kilteni & Ehrsson, 2017b). Further, when the rubber hand was placed at a distance, but subjects' hands were aligned (A situation that normally produces sensory attenuation), it led to a significant decrease in attenuation (ibid.). This provides an example of how forward models continually estimate the state of our body and the world.

There are several ways of learning through which we adjust motor behaviour and predictions (Wolpert et al., 2011). Even just by using the motor system and making repetitive reaching movements in one random direction biases the system towards that direction in the future, this is termed use-dependent learning (ibid., p. 744).

Another way for the system to learn is through reinforcement learning: By making predictions about the future state when executing a movement, forward models correctly tell us if we reached the desired state. If the desired state is connected with a reward signal it can reinforce the motor-behaviour that led to this state (ibid, p. 743). This way of learning, however, is slow as the reward signal inherently provides little information (Success or failure).

A third process of learning is through error correction, so called error-based learning. This has been shown in many adaptation paradigms, where participants adjust their motor behaviour to different perturbations (ibid). When the forward model makes sensory predictions the comparison process between predicted and actual outcome returns the discrepancy between the two. This error signal can inform the motor system of necessary adjustments to reduce error, however, this can only be determined with some amount of noise, one error can lead to several different adjustments (ibid). In a hand-reaching experiment with visual and spatial perturbations Wei and Kording (2010) discovered that noise in feedback decreases the rate of adaptation while uncertainty of estimated state increases the rate of adaptation. Similar differences in rates of motor-learning has been found to be affected by a fast learning process which quickly adapts but also quickly “forgets” and a slow learning process which retains information over a wider time scale (Smith, Ghazizadeh, & Shadmehr, 2006). These fast and slow processes have been linked to explicit and implicit learning proesses in a visuomotor adaptation task by striking similarities in their adaptation rates (McDougle, Bond, & Taylor, 2015). Explicit learning, defined as the target-error, happens when participants are instructed how to counter a given perturbation and their adaptation is thus faster (Taylor, Krakauer, & Ivry, 2014). Implicit learning is driven by the previously described sensory prediction error signal provided by the discrepancy between predicted and actual sensory feedback. This learning is slow and monotonic and occurs on a trial-to-trial basis by correcting prediction error from each trial (ibid; Wolpert et al., 2011; Wolpert & Flanagan, 2001, p. 729; Krakauer & Mazzoni, 2011, p. 637).

Sensory attenuation and adaptation has also been studied using MEG/EEG approaches. Using paradigms that measure the activity in auditory cortex while participants trigger a sound by pressing a button. Schafer and Marcus (1973) found a significant difference between the amplitudes of a self-generated stimuli vs an externally generated sound in several components. This mirrors the classic sensory attenuation effect; The salience of an external stimuli is much greater than that of the self-produced stimuli. A later study tested the hypothesis that this observation of differences in amplitude is caused by prediction error (SanMiguel, Saupe, & Schröger, 2013). Participants through three conditions, two different sound conditions and a no sound condition (ibid, p. 2). In the sound conditions participants either triggered the same sound or a random sound which in both conditions would be randomly omitted. The logic being that the motor system can consistently predict the single repeated sound but not the randomly different sounds (ibid.). They found that during the single-sound condition there was still activity in auditory cortex during sound omission trials, which reflects the neural code of the sensory prediction (ibid, p. 6). Importantly, no such difference was observed when sound was omitted in the random sound condition, as no stable representation and prediction could be formed of the self-triggered stimuli (ibid). This approach has also been used to study whether motor-imagery represents actions in the same way as executed actions by demonstrating sensory attenuation of sensory consequences during imagined action (Whitford, Jack, Pearson, Griffiths, Luque, Harris, Spencer, & Le Pelley, 2017; Tian, Ding, Teng, Bai, & Poeppel, 2018). However, by using speech they do not have a control measure to ensure no speech muscles were subtly activated during covert conditions.

While learning and updating internal forward models have been rigorously tested with different spatial and visuomotor adaptation paradigms there has been little use of lag adaptation in behavioural studies on sensorimotor learning and sensory attenuation. However, MEG and EEG experiments have been used to investigate the effects of temporal perturbation on the attenuation of the resulting Sensory Evoked Potentials (SEPs). In these studies participants trigger a sound by the press of a button, they are then trained for a variable amount of trials with either no delay between the press and the sound or a 100 ms delay between their press and the sound (Aliu, Houde, & Nagarajan, 2009; Elijah, Le Pelley, & Whitford, 2016; Cao, Veniero, Thut, & Gross, 2017). They then measure and compare the M100/N1 component between conditions with or without a delay. In their initial findings there was significant differences between the amplitude of the N1 component in conditions with immediate and delayed feedback (Aliu et al., 2009; Elijah et al., 2016). However, when trained with a delay this significant difference in amplitude disappeared between the conditions, suggesting motor-induced suppression of delayed feedback equal to immediate feedback (ibid.). These studies of physiological attenuation suggest a similar process of gradual learning through error correction in sensory predictions. However, studies measuring physiological attenuation in the amplitude of evoked potentials remain relatively isolated from studies using behavioural measures of sensory attenuation (Palmer, Davare & Kilner, 2016). While it is tempting to conclude that they both reflect the same predictive neural processes, it is suggested that they have different underlying neurophysiological correlates, and that the relationship between physiological and perceptual sensory attenuation is not straightforward (Ibid).

In the present study we aim to investigate this role of temporal recalibration in the sensory predictions made by an internal forward model. Using a design that ensures recalibration with an initial exposure block followed by re-exposure after each response (Cai, Stetson, & Eagleman, 2012). However, we use the Point of Subjective Equality (PSE) as a measure similar to Bays and colleagues (2005) instead of the Point of Subjective Simultaneity (PSS). We hypothesize that shifts in attenuation reflects "recalibration" of the sensory predictions by an internal forward model. Particularly we theorize that the usual patterns of attenuation reverse after delay exposure, i.e. delayed touch is attenuated after exposure to a delay and immediate touch is not attenuated after exposure.

Methods

A total of 120 subjects, 30 participants per experiment, participated across four different experiments. Sample size was based on previous studies using exposure to systematic delays between action and sensory consequence (Cai et al, 2012; Stetson et al, 2006). Participants were recruited from the general Stockholm area, using flyers, advertisements on a Swedish website for research (www.studentkaninen.se), and via advertisements on various Facebook groups.

In all of the experiments, subjects rested their left hand with the palm of the hand facing upwards and their left index finger placed in a molded support. A cylindrical probe made of aluminum with a flat surface (20 mm diameter) rested on the pulp of the subjects left index finger. The probe was attached to, and controlled by, a torque motor (Maxon EC Motor EC 90 Flat manufactured in Switzerland). A small commercially available force sensor (FSG15N1A, Honeywell Inc.; diameter 5mm; minimum resolution, 0.01 N; response time, 1 ms; measurement range, 0-15 N) was placed inside the probe in order to measure the force generated by the motor. A laptop computer using Linux Ubuntu controlled the motor. Commands were sent from the laptop to an Arduino board that send commands to a second controller connected to the motor. The system has an intrinsic delay of approximately 35 milliseconds including the rising time of the applied force.

A force sensor was placed inside a similar cylindrical probe, mounted on top of a small wooden support, was put over their left index finger. Participant sat with their right-hand hovering above this sensor awaiting an auditory cue to press the sensor with their right index finger. To ensure the comfort of subjects we had several pads of foam available that participants could place freely, before the start of the experiment, for both their hands and forearms to rest on.

The participants’ hands, forearms, and the torque motor were placed behind a screen to prevent view during all conditions. Participants were also requested to visually fixate on a cross, which was located at a 2 meters distance on the wall opposite to them in their eye height. On the left and right side of the cross, a left-pointing arrow accompanied by “first force stronger” and a right-pointing arrow accompanied by “second force stronger” was placed to serve as a reminder for participants when using the foot-pedal during the psychophysical task described below.

Further, subjects wore headphones playing white noise during the experiment to prevent unwanted sounds, created either by the experimenter clicking a mouse button to initiate trials, from the motor during presented taps, or by participants’ right-hand tap, being used as cues for the task. The noise level was adjusted to the individual participant’s hearing before the start of the experiment. The Regional Ethical Review Board of Stockholm approved all experiments (Approval #:2016/445-31/2).

Experimental Procedure

The experiment consisted of five conditions: Four active movement conditions and a passive condition (no movement) as a baseline.

Active Conditions

The active conditions consisted of the experiment consisted of *exposure trials* and *response trials*. During *exposure trials*, participants were instructed to, upon hearing an auditory cue (a sine wave of 1000 Hz lasting 100 ms), tap the sensor placed over their left index finger as soon as possible with their right index finger (active tap). When participants tapped the sensor, they would trigger the motor and receive a single 2 N tap lasting 100 ms on their left index finger (test tap). This test tap could appear either immediately (without any additional delay other than the intrinsic delay of the system) after the active tap, to simulate self-touch, or with an added 100 ms delay (*exposure* delay).

During *response* trials participants reacted to the same auditory cue, as heard during exposure trials, upon which they would trigger the test tap with their active tap on the Sensor. The test tap would again appear either immediately or after a small 100 ms delay (*test* delay). A second externally triggered force (comparison tap) followed the test tap of the motor initiated by the participant's active tap after a random delay between 800 ms and 1500 ms after. The intensity of the comparison tap varied between 1-3 N (1, 1.5, 1.75, 2, 2.25, 2.5, or 3). Participants were prompted, after a *response*-trial, to perform a forced choice between the two taps. They had a 2 second window, cued by a tone (a sine wave of 1500 Hz lasting 2000 ms), to indicate which tap felt stronger to them: the test tap (first tap) or the comparison tap (second tap). Participants were instructed to move a foot pedal left or right (first force stronger or second force stronger) during the tone to indicate their choice. Participants had the option to change their indicated answer shortly after the tone and before the next trial.

Each condition consisted of 70 *response* trials corresponding to 10 repetitions for each of the seven varying forces. The order of forces was randomized for each participant. Each response trial was preceded by five *exposure* trials to re-expose participants after a *response* trial. Subjects went through a small block only consisting of exposure trials in the beginning of each condition.

The four active conditions corresponded to the four combinations of *exposure* delay and *test* delays. So, a condition of no delay in neither exposure nor delay [0 ms, 0 ms]; a condition with *exposure* delay but no *test* delay [100 ms, 0 ms]; a condition with no *exposure* delay but an added *test* delay [0 ms, 100 ms]; and a condition with both *exposure* delay and *test* delay [100 ms, 100 ms]. Subjects went through a small block only consisting of exposure trials in the beginning of each condition. Participants were briefly taught how to press the sensor with their right index finger in a short training session before the beginning of the experiment. This was done to avoid participants adopting different tapping strategies and to ensure that they did not press to hard or too soft.

Baseline Condition

During the passive condition participants sat passively with their right index finger resting on the button as they received two successive taps on their left index finger. The initial test tap was presented 500 ms after the same auditory cue as heard during active conditions and the variable comparison tap would be presented randomly between 800-1500 ms after the test tap. Participants then went through the same response procedure as in the active conditions. As it assessed sensory attenuation without movement this condition had only *response* trials. The baseline condition consisted of 105 response trials with 15 repetitions of the seven different intensities (1 N, 1.5 N, 1.75 N, 2 N, 2.25 N, 2.5 N, or 3 N). Other groups have previously used this psychophysical paradigm to measure the degree of sensory attenuation (Bays et al, 2005).

Participants never received any feedback concerning their performance in the two-alternative forced-choice task. The order of conditions and the order of presented forces was randomized for each participant to avoid order effects.

Data and Statistical Analysis

The collected responses from each participant in each condition was fitted with a logistic regression model where α represents the intercept and β the slope (Eq. 1):

$$f(x) = 1/1 + \exp(-(\alpha + \beta x)) \quad \textbf{(1)}$$

The fitting was done using a glm function with a logit link function in R 3.4.0. We extracted the point of subjective equality (PSE) from the fitted curve of each participant for each condition (Fig. 1.). The PSE corresponds to the point where the participant perceives the test tap (Fixed at 2 N) to be equal to the comparison tap ($p = 0.5$). Further, we extracted the Just Noticeable Difference (JND). The JND is the intensity of the comparison tap where the probability of a participant perceiving the comparison tap as stronger is equal to 0.75.

Figure 2. A subject’s data fitted with a logistic model

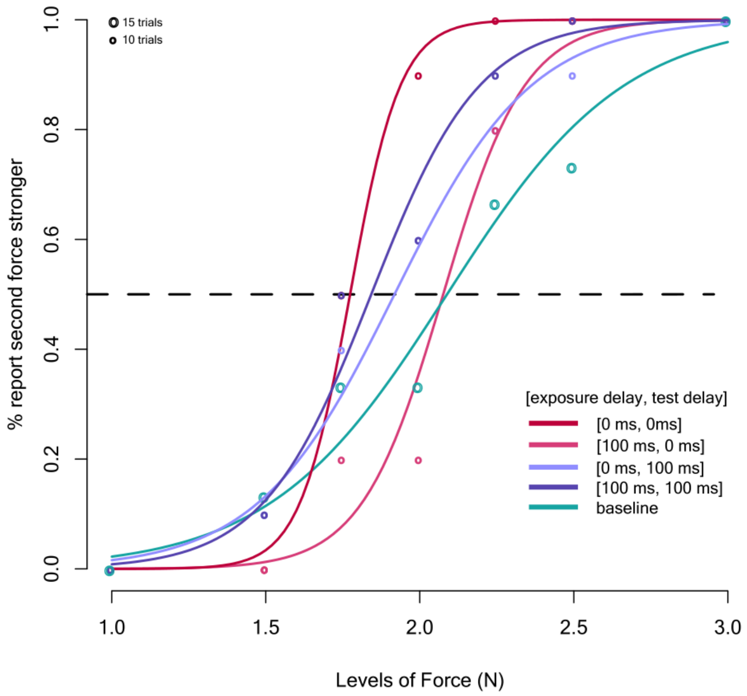

Figure 2. The data of a representative participant fitted with a logistic regression model as shown in equation 1. The dashed line intersects the point where the model puts 0.5 probability (50%) that the participant choses the second of the two forces as stronger. From this point, we infer that both forces are perceived as equal and we extract it as the point of subjective equality (PSE).

Normality of PSE distributions was tested using Shapiro-Wilk tests and the variance equality with F-tests. Planned comparisons were then performed with either paired t-tests or Wilcoxon signed-rank tests depending on the result of above tests. As hypothesized we were mainly interested in seeing the shifts in perception of immediate touch and delayed touch when exposed to either immediate or delayed touch. Thus, the main comparisons drawn are between a *test* delay and the two different conditions of exposure delay (100 ms exposure delay, 0 ms exposure delay) as well as the baseline that assesses the participants’ passive perception of the forces. All statistical tests done were two-tailed.

Experiment one

Thirty naïve participants (17 females and 13 males) between the ages of 20-32 (mean age = 24.6, SD = 4.2) participated after providing written informed consent. Participants handedness (27 right-handed and 3 ambidextrous) were assessed with the Edinburgh Handedness Inventory (Oldfield, 1971). None of the participants knew the hypotheses of the experiment and they were unable guess the purpose of the experiment either before or after the completion of the experiment. One participant was excluded from the statistical analysis because of a problematic fit of baseline condition, making N = 29.

Following Cai and colleagues experimental design (2012, p. 6), to make participants adapt to a delay, we had a brief pre-adaptation block of 50 *exposure* trials which was then followed by 5 trials of re-exposure before each *test* trial. For this experiment, we injected a 200 ms delay between participants' active tap and the test tap they received during delay conditions.

Following temporal recalibration research there is some uncertainty as to which delays yields the largest lag adaptation. Stetson and colleagues (2006) found the largest shifts of participants' point of subjective simultaneity using a 100 ms delay. However, Heron and colleagues (2009) found considerably larger shifts in tactile modality using a 200 ms delay between action and sensory consequence. We used a 200 ms delay between active tap and the test tap for this experiment

Participants went through five conditions: A no delay condition [0 ms, 0 ms], an exposure delay condition [200 ms, 0 ms], a test delay condition [0 ms, 200 ms], a constant delay condition [200 ms, 200 ms], and a passive condition. Each condition lasted approximately 10-12 minutes making the total time for the experiment around an hour. Participants had the option to take a small break between each condition. The order of conditions and forces were randomized.

We collected the 70 data points for each active condition and 105 data points for the baseline condition. We then fitted the data points with a logistic model to gather the point of subjective equality (PSE) between the test tap and the comparison tap. We then compared the mean PSE for each condition by using paired t-tests (see methods).

Here we are using attenuation as a measure of recalibration rather than the point of subjective simultaneity as used by previous temporal recalibration studies. Thus, we expect to replicate the already known results from other studies using sensory attenuation as a measure (Blakemore et al, 1999; Bays et al, 2005). The internal forward model of subjects predicts the immediate tap caused by self-action resulting in attenuated somatosensory perception of the test tap. It has also previously been shown when the temporal prediction made by the forward model is violated by a small delay (100 ms, 200 ms) less attenuation is observed in subjects.

We hypothesize that the observed mean PSE of the no delay condition [0 ms, 0 ms] will be significantly lower compared to the mean PSE observed in the passive condition and the test delay condition [0 ms, 200 ms]. As sensory evidence is gathered in the exposure delay conditions [200 ms, 0 ms; 200 ms, 200 ms] we expect that the mean PSE will shift in the opposite direction compared to their no delay counterparts [0 ms, 0 ms; 0 ms, 200 ms] i.e. there will be less or no attenuation of immediate touch and attenuation of the delayed test tap during delay exposure.

Experiment one: Results

When exposed to the immediate test tap (0 ms *exposure* delay) we observed significant attenuation only in the immediate test tap [0 ms, 0 ms] (M = 1.82, SD = 0.16) when compared to the baseline (mean PSE = 1.96, SD = 0.095), when using a paired t-test, $t(28) = 4.52$, mean difference = 0.13, 95% confidence interval [CI] = [0.19, 0.07], $p < 0.001$. We did not observe significant differences between the delayed test tap (mean PSE = 1.92, SD = 0.13) and the baseline (paired t-test between test delay condition [0 ms, 200] and baseline), $t(28) = 1.5$, mean difference = 0.04, 95% confidence interval [CI] = [-0.014, 0.09], p = 0.14. As previously shown by other studies investigating sensory attenuation subjects felt the immediate test tap [0 ms, 0 ms] significantly less intense compared to the delayed test tap [0 ms, 200 ms] during immediate exposure with a paired t-test, $t(28) = 3.04$, mean difference = 0.09, 95% confidence interval [CI] = [0.16, 0.03], p = 0.005.

Figure 3. Results

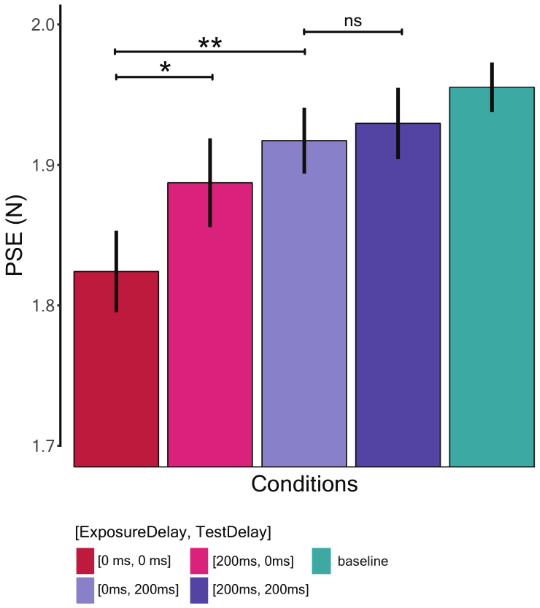

Figure 2. Results for the first experiment. Shown here is the mean PSE for each condition with bars displaying ± standard error. Important comparisons are displayed (*p < 0.05, **p < 0.01, ns = not significant).

When exposed to an injected delay between the active tap and the test tap participants felt the immediate test tap (mean PSE = 1.89, SD = 0.17) significantly more intense compared to the no delay condition (paired t-test between [0 ms, 0 ms] and [200 ms, 0 ms]), *t*(28) = 2.16, mean difference = 0.06, 95% confidence interval [CI] = [0.123, 0.003], p = 0.04. The exposure delay condition [200 ms, 0 ms] was however significantly different from baseline somatosensory perception when compared with a paired t-test, *t*(28) = 2.22, mean difference = 0.07, 95% confidence interval [CI] = [0.130, 0.005], p = 0.034. While they felt the immediate test tap less intense after delay exposure, it was still attenuated. This suggests that the predictions of the forward model shifted towards a delay reflected in this rise in PSE. Nevertheless, subjects did not completely forget to predict the immediate tap. We expected that with a consistent exposure to a delay, participants would feel the delayed test tap (mean PSE = 1.93, SD = 0.14) attenuated compared to the delayed test tap during exposure to the immediate test tap. However, when we compared [200 ms, 200 ms] and [0 ms, 200 ms] with a paired t-test this was not the case, *t*(28) = 0.51, mean difference = 0.01, 95%

confidence interval [CI] = [-0.04, 0.06], p = 0. 61. The delayed test tap [200 ms, 200 ms] was not attenuated compared to baseline, *t*(28) = 0.91, mean difference = 0.026, 95% confidence interval [CI] = [0.08, -0.03], p = 0.37.

We successfully managed to replicate previous known results, confirming that this design accurately measures sensory attenuation. In this experiment, we demonstrate that when exposed to a delay of 200 ms, between a movement and its sensory consequence, the immediate test tap becomes more salient, yet still attenuated, than when subjects received no exposure delay. Presumably, because the prediction of the forward model is adjusted in favor of a delay. However, we do not see any conclusive evidence of this as the delayed tap is not attenuated. The comparator has also been associated with the feeling of agency (Synofzik et al, 2008). The consistent mismatch between predicted and actual sensory feedback during test delay observed in this experiment indicates no recalibration and no feeling of agency over the test tap. Previous studies show that there is a diminished effect of recalibration with increasingly large delays (Stetson, 2006, p. 654; Heron et al. 2009, p. 3). With larger delays it is also more likely that a subject considers the resulting sensory consequence as something not directly caused by their action (ibid.).

While the relationship between sense of agency and sensory attenuation is rather complex, there is some evidence to suggest that the sense of agency or the belief that a sensory consequence is self-caused is a pre-requisite for sensory attenuation to occur (Desantis et al, 2012; Gentsch & Schütz-Bosbach, 2011). Although it is debatable, at what point this change in causality judgement of a sensory consequence occurs, our findings could suggest that a 200 ms delay is beyond this point. To investigate further we repeated the same experiment using a 100 ms delay over a 200 ms delay.

Experiment two

Thirty naïve participants (17 females and 13 males) between the ages of 20-32 (mean age = 25.3, SD = 3.6) participated after providing written informed consent. Participants handedness (27 right-handed and 3 ambidextrous) were assessed with the Edinburgh Handedness Inventory (Oldfield, 1971). None of the participants knew the hypotheses of the experiment and they were unable to guess the purpose of the experiment either before or after the completion of the experiment.

Using the exact same design as previous experiment. Participants did five separate conditions, four of them active and one of them passive, where we collected their point of subjective equality (PSE) for each condition by fitting the data points (70 in the active conditions, 105 in the passive baseline) with a logistic regression. The four active conditions were split into all possible combinations of exposure delay and test delay: No delay [0 ms, 0 ms]; test delay only [0 ms, 100 ms]; exposure delay only [100 ms, 0 ms]; and constant delay [100 ms, 100 ms]. The no movement condition acted as a baseline for subjects' somatosensory perception. The order of conditions and forces was randomized for each participant. Each condition lasted approximately 10-12 minutes and participants had a small break between each condition to stretch their fingers and to prevent tiredness. The entire session lasted approximately 60 minutes.

We reduced the delay used from 200 ms to 100 ms reasoning that a 200 ms delay is a too large delay for subjects to associate the triggered test tap as a direct consequence of their active tap. At the beginning of each condition, subjects still had 50 trials of exposure followed by five trials of re-exposure before each response trial.

Testing the same hypotheses as previous experiment, we expect again to replicate previously shown results. We hypothesize that exposure to a consistent delay will shift the usual patterns of attenuation in the opposite direction, i.e. participants will not attenuate the immediate tap and attenuate the delayed tap because subjects recalibrated their internal forward model. We expect a significant decrease in the mean PSE of the no delay [0 ms, 0 ms] and constant delay [100 ms, 100 ms] condition compared to the mean PSE observed in the baseline condition. Further, we predict a significant increase in mean PSE of the immediate touch during delay exposure [100 ms, 0 ms] when compared to the no delay condition [0 ms, 0 ms].

Experiment two: Results

During exposure to immediate touch (0 ms *exposure* delay) we observed only attenuation of the immediate test tap [0 ms, 0 ms] (M = 1.86, SD = 0.16) when compared to the baseline (M = 1.99, SD = 0.13) using a paired t-test, *t*(29) = 3.295, 95% confidence interval [CI] = [0.204, 0.048], M = 0.13, p = 0.003. As expected, we successfully replicated previous findings of other studies; the immediate tap felt significantly less intense as a result of forward model prediction based on the movement. We observed no significant differences between the delayed test tap [0 ms, 100 ms] (M = 1.95, SD = 0.15) when compared to the baseline condition using a paired t-test, *t*(29) = 0.897, 95% confidence interval [CI] = [-0.043, 0.109], M = 0.03, p = 0.38. While previous studies did find significant differences during conditions with an injected delay and a passive condition, the additional sensory evidence in favour of immediate touch yielded by the five re-exposure trials could explain this finding. As expected from previous studies, the immediate test tap [0 ms, 0 ms] felt significantly less intense compared to the delayed test tap [0 ms, 100 ms], *t*(29) = 3.82, 95% confidence interval [CI] = [0.143, 0.0431], M = 0.09, p < 0.001.

Figure 4. Experiment two results

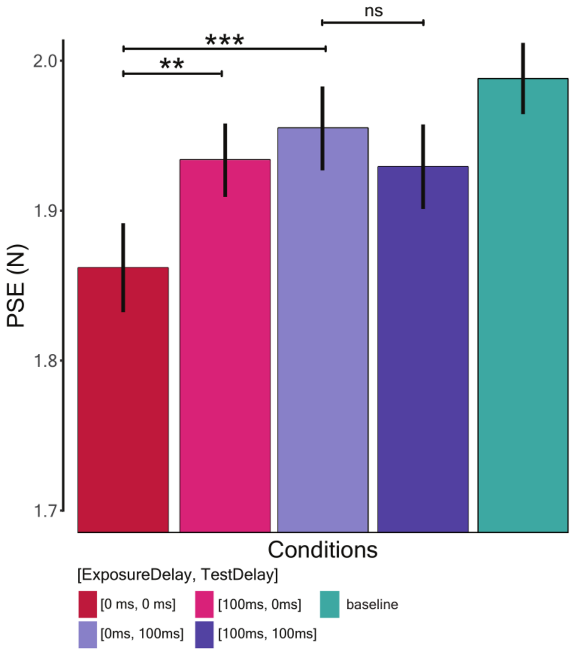

Figure 4. The mean PSE gathered for each condition for the second experiment with bars displaying ± standard error. Only the important comparisons are displayed (**p < 0.01, ***p < 0.001, ns = not significant.

Again, when participants were exposed to a consistent 100 ms delay during exposure trials this pattern of attenuation reversed. Subjects felt the immediate test tap during delay exposure [100 ms, 0 ms] (mean PSE = 1.93, SD = 0.13) significantly stronger compared to the no delay condition [0 ms, 0 ms] *t*(29) = 2.86, mean difference = 0.07, 95% confidence interval [CI] = [0.12, 0.02], p < 0.01. Additionally, the immediate test tap was no longer attenuated even when compared to baseline using a paired t-test, *t*(29) = 0.15, mean difference = 0.05, 95% confidence interval [CI] = [-0.02, 0.13], p = 0.15. We did not observe the same reversal pattern when comparing mean PSE of the delayed test tap during exposure (mean PSE = 1.93, SD = 0.15) [100 ms, 100 ms] and no exposure [100 ms and 100 ms], *t*(29) = 1.22, mean difference = 0.025, 95% confidence interval [CI] = [-0.017, 0.07], p = 0.23. However, there was a trend towards attenuation of the delayed test tap during delay exposure [100 ms, 100 ms] when compared to the baseline, *t*(29) = 1.70, mean difference = 0.06, 95% confidence interval [CI] = [-0.01, 0.13], p = 0.09972.

Figure 5. Shift in attenuation of the immediate tap

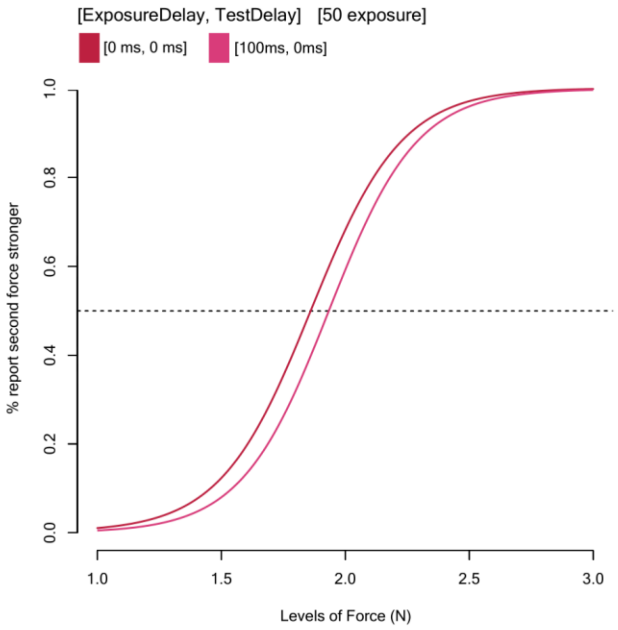

Figure 5. The logistic regression fitted using the group data for the no delay condition and the exposure delay condition. Mean PSE and Mean JND for each condition was used to make the fit. Participants “unlearn” the prediction of the immediate test tap when they are exposed to a 100 ms delay between their active tap and the test tap they receive.

In experiment two, we successfully managed to replicate previous shown results in the literature and the results from experiment one, suggesting that the internal forward model is recalibrating its temporal predictions during delay exposure. Because the expected shift in attenuation of the delayed test tap was not observed, there are still alternative conclusions, which can be drawn from this set of data. One possible explanation is that the mismatch between prediction and the sensory consequence is caused by general uncertainty added by the delay and not necessarily an update of the internal forward model. However, upon further inspection, by comparing the Just-Noticeable Difference (JND), which is the point of 0.75 probability that participants judge the comparison tap as stronger, it appears that there were no significant differences in certainty between the two conditions. A paired t-test was done between the mean JND of the no delay condition [0 ms, 0 ms] (mean JND = 0.183, SD = 0.8) and the exposure delay condition [100 ms, 0 ms] (mean JND = 0.178, SD = 0.07), *t*(29) = 0.30, mean difference = 0.005, 95% confidence interval [CI] = [-0.03, 0.04], p = 0.77. Discriminability remained the same thus making uncertainty an unlikely explanation for the difference between the two conditions. Further, we see a trend in attenuation of the delayed test tap compared to the baseline, which leans towards our hypothesis. However, it is not enough evidence to conclude that the internal forward model has recalibrated its predictions of timing between action and consequence.

As noise and uncertainty is always a factor in sensorimotor control the system relies upon Bayesian inference to accurately represent probabilities of outcomes in order to successfully predict the most likely outcome of an action (Kording & Wolpert, 2006, p. 319). The prior experiences of timing between action and consequence, which should be experienced as immediate, is continually weighted against incoming sensory feedback in order to make an inference about the probable result of an upcoming movement. The error between the predicted outcome and the actual outcome returns an error, which can be used to update future predictions (Wolpert et al, 2011, p. 742). While such error-based learning usually can lead to rapid trial by trial learning, it can also be more gradual (ibid; Taylor, Krakauer & Ivry, 2014, p. 3023; Wolpert & Flanagan, 2016, p. 8).

In a visuomotor adaptation task done by Taylor and Ivry (2011), participants were instructed to make rapid reaching movements towards a visually displayed target by sliding their hands along the surface of a table. After a set amount of trials to familiarize subjects with the task participants were taught a specific aiming strategy. After some practice, a 45-degree visuomotor perturbation was introduced. Participants then had 320 trials to correct the resulting endpoint error and successfully reach the designated target. When participants relied purely on the visual landmark and their own error correction, it took approximately 100 trials before successfully adapting to the spatial perturbation (ibid; Taylor et al, 2014, p. 3023). Thus, the kind of implicit error-based learning where, a perhaps unconscious, adjustment of the predictions of a forward model can be rather slow and gradual. Similarly, MEG/EEG studies that found a cortical suppression of the M100/N1 component in auditory cortex in trials with a 100 ms delayed tone triggered by participants’ button press only observed attenuation within 300 trials (Cao et al., 2017; Aliu et al., 2009; Elijah et al., 2016).

One possibility that we only begin to see a trend in attenuation of the delayed tap during delay exposure, is that there has not been enough sensory evidence for the subjects to adjust the temporal prediction of their internal forward model. To test if further sensory evidence is required before subjects updated their forward model, we conducted the same experiment again. This time we adjusted the amount of exposure participants received.

Experiment three

Thirty new naïve participants (13 females and 17 males) between the ages of 19-35 (mean age = 24.3, SD = 4.5) participated after providing written informed consent. Participants handedness (27 right-handed and 3 ambidextrous) were assessed with the Edinburgh Handedness Inventory (Oldfield, 1971). None of the participants knew the hypotheses of the experiment and they were unable to guess the purpose of the experiment either before or after the completion of the experiment.

Retaining the same design as in previous experiments. We collected a subjects’ point of subjective equality (PSE) in five different conditions by fitting the data points with a logistic regression (70 trials in active conditions, 105 trials in the baseline condition). The conditions where the same as in the previous experiment also using a 100 ms delay between participants’ active tap and the test tap. We had a no delay condition [0 ms, 0 ms], a test delay condition [0 ms, 100 ms], an exposure delay condition [100 ms, 0 ms], a constant delay condition [100 ms, 100 ms], and finally a passive condition serving as a baseline for participants' somatosensory perception.

For this experiment, participants were exposed to 200 trials of either no delay or delay before starting the block of five re-exposure trials before each response trial. We predict that the added amount of initial exposure used in this experiment should yield enough incoming sensory evidence for subjects to update their forward model and predict the delayed test tap.

With the increased amount of trials, each condition lasted between 15-18 minutes. The entire experiment lasted approximately 80 minutes. Participants had a small break between each condition where the experimenter asked them to remove their fingers from the setup and stretch them. This was done to prevent tiredness and potential numbness in their left index finger. The order of conditions and forces was randomized for each participant.

Testing the same hypotheses as previous experiments, we expect again to replicate previously shown results. We hypothesize that with the additional exposure to a consistent delay will shift the usual patterns of attenuation in the opposite direction, i.e. participants will not attenuate the immediate tap and attenuate the delayed tap because subjects recalibrated their internal forward model. We expect a significant decrease in the mean PSE of the no delay [0 ms, 0 ms] and constant delay [100 ms, 100 ms] condition compared to the mean PSE observed in the baseline condition. Further, we predict a significant increase in mean PSE of the immediate touch during delay exposure [100 ms, 0 ms] when compared to the no delay condition [0 ms, 0 ms].

Experiment three: Results

Again, as expected, we found significant attenuation of the immediate tap when comparing the no delay condition (mean PSE = 1.78, SD = 0.11) [0 ms, 0 ms] to the baseline (mean PSE = 1.997, SD = 0.12). Comparison was made using a paired Wilcoxon signed rank test as the Shapiro-Wilk normality test was $p = 0.05$, $V = 32$, $p < 0.001$. As in previous studies, we observed a significant difference between the immediate and the delayed test tap [0 ms, 100 ms] (mean PSE = 1.91, SD = 0.12) during no delay exposure conditions, *t*(29) = 4.73, mean difference = 0.11, 95% confidence interval [CI] = [0.15, 0.06], p < 0.001.

Figure 6. Experiment three results

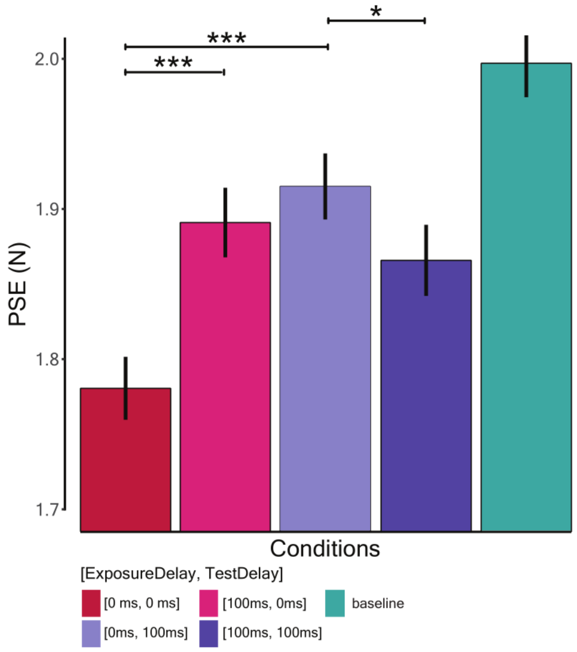

Figure 6. The mean PSE gathered from each condition with bars displaying ± standard error. Only the important comparisons are displayed (*p < 0.05, ***p < 0.001, ns). With the added trials of exposure subjects now attenuate the delayed test tap.

The reversal of the attenuation "pattern" of the immediate test tap is again replicated in this experiment. With the added exposure we find a significant shift between the immediate tap during no delay exposure [0 ms, 0 ms] and the immediate tap during delay exposure [100 ms, 0 ms] (mean PSE = 1.89, SD = 0.13) when comparing with a paired t-test, *t*(29) = -6.77, mean difference = 0.13, 95% confidence interval [CI] = [0.18, 0.09], p < 0.001. Unlike the previous experiment, the immediate tap during delay exposure [100 ms, 0 ms] was still significantly different from participants' passive perception of the forces, *t*(29) = 4.78, mean difference = 0.11, 95% confidence interval [CI] = [0.15, 0.06], p < 0.001.

Figure 7. Shift in attenuation of the immediate test tap

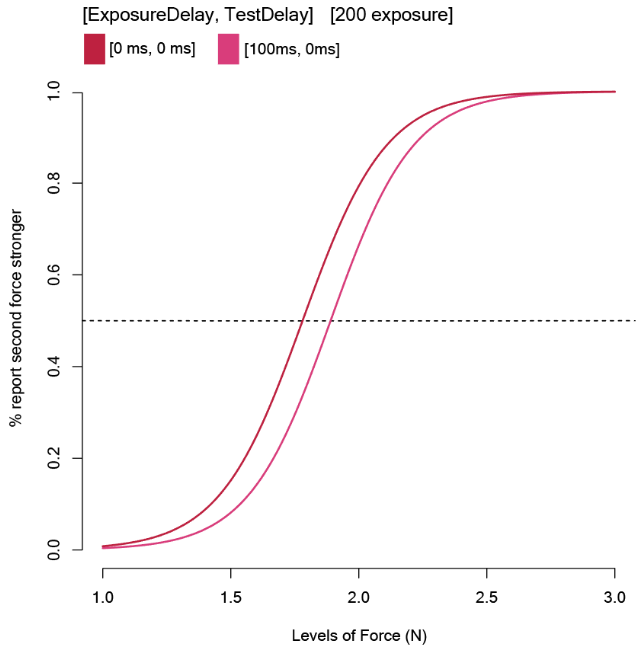

Figure 7. The logistic regression fitted using the group data of the immediate test tap during exposure to no delay or a delay. Mean PSE and Mean JND for each condition was used to make the fit. Participants "unlearn" the prediction of the immediate test tap when they are exposed to a 100 ms delay between their active tap and the test tap. As demonstrated by the curve shifting towards the right during delay exposure.

Importantly, we see the opposite shift in attenuation of the delayed test tap during no delay exposure [0 ms, 100 ms] and delay exposure [100 ms, 100 ms] (mean PSE = 1.86, SD = 0.13), using a paired t-test, $t(29) = 2.65$, mean difference = 0.05, 95% confidence interval [CI] = [0.01, 0.09], p = 0.013. Confirming, that given enough exposure for error-based learning to take effect, subjects gradually update their internal forward model and predict the delayed tap.

Figure 8. Shift in attenuation of the delayed test tap.

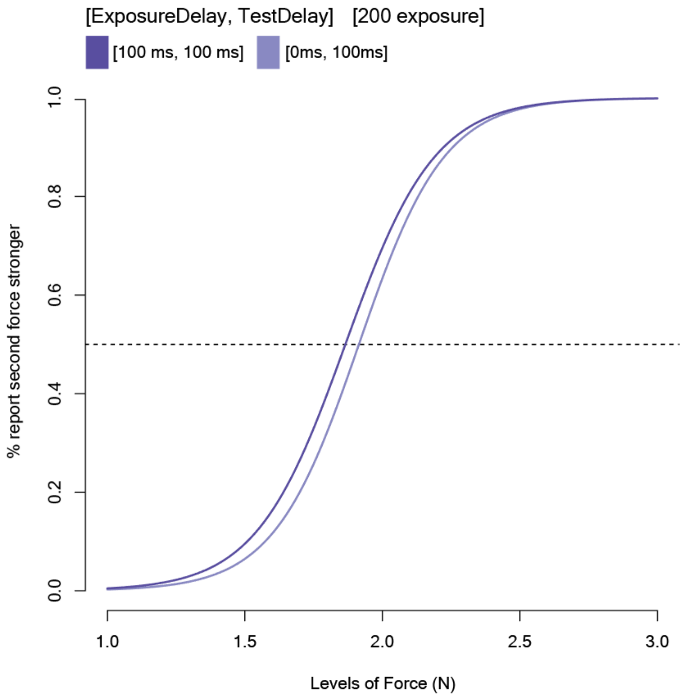

Figure 8. The logistic regression fitted using the mean PSE and mean JND at 75% of the delayed test tap during exposure to immediate touch or during exposure to delayed touch. The left shift of the curve during constant delay from the curve during no delay exposure demonstrates that participants now predict and attenuate the delayed test tap.

Interestingly, all active conditions were significantly different from the baseline in this experiment including the delayed test tap during immediate exposure [0 ms, 100 ms] (paired t-test: *t*(29) = 3.60, mean difference = 0.08, 95% confidence interval [CI] = [0.12, 0.03], p = 0.001). This is more in tandem with previous studies where the act of movement itself requires a vast delay before perceived equally to passive experience of the given sensory consequence (Bays et al, 2005). Yet, it is surprising given the results of the two previous experiments.

In the third experiment, we replicate results from the previous two experiments. Importantly, with the additional trials of exposure in the beginning of the experiment participants updated their internal forward model. Subjects "unlearned" to predict the immediate tap as indicated by the positive shift in PSE while they learned to reliably predict the delayed tap as indicated in the negative shift of the delayed tap. In a motor adaptation study by Wei and Kording (2010), they had participants do a reaching task where they would adapt trial-by-trial to visual perturbations. One of the hypothesis was that with increased amount of uncertainty in sensory feedback slower adaptation would be observed. In the study of Ivry and Taylor (2011) mentioned earlier participants performance were still improving past the point of the 100 trials mentioned. The small temporal delay used in this study in combination with a somatosensory feedback being a short 100 ms tap and the overall nature of the task can mean that feedback is uncertain and lag adaptation is slower. To investigate further if more added exposure would lead to a bigger shift in attenuation we repeated the same experiment while adding even more trials to the initial exposure period before the onset of response trials.

Experiment four

In experiment four, we changed the amount of trials in the initial exposure block from 200 trials to 500 trials reasoning that with the added amount of exposure participants had even more trials to gradually adapt their forward model to predict the delayed tap. We expect to observe a larger shift in attenuation of the delayed than observed in previous studies.

Thirty naïve participants (15 females and 15 males) between the ages of 18-32 (mean age = 24.6, SD = 3.7) participated after providing written informed consent. Participants handedness (27 right-handed and 3 ambidextrous) were assessed with the Edinburgh Handedness Inventory (Oldfield, 1971). None of the participants knew the hypotheses of the experiment and they were unable to guess the purpose of the experiment either before or after the completion of the experiment.

Using the same task and design as experiment one, two, and three we collected the point of subjective equality (PSE) after 500 trials of exposure. The PSE for each condition was collected by fitting a logistic regression to the data points of each condition (70 response trials in active conditions, and 105 response trials in the passive condition). Participants did the same five conditions as previous experiments: No delay [0 ms, 0 ms], test delay [0 ms, 100 ms], exposure delay [100 ms, 0 ms], constant delay [100 ms, 100 ms], and the passive condition acting as a baseline of somatosensory perception. Order of forces and order of conditions were randomized for each participant. Each condition lasted between 20-22 minutes. Participants had a short break between each condition were the experimenter asked them to remove their hands from the motor and stretch them in an attempt to avoid tiredness and numbness. The entire session lasted between 90-105 minutes.

In this experiment, we're testing the same hypothesis as previous experiments. We expect to replicate previous shown results, particularly the results of experiment three. Additionally, we hypothesize that with the additional trials subjects will more accurately recalibrate and update their internal forward model to predict the delayed test tap. As in previous experiments, we expect a significant decrease in mean PSE during no delay exposure between the immediate [0 ms, 0 ms] and the delayed [0 ms, 100 ms] tap during response trials. We predict that during delay exposure this pattern of attenuation of the immediate [100 ms, 0 ms] and the delayed [100 ms, 100 ms] test tap will reverse. We expect a significant increase in mean PSE of the exposure delay [100 ms, 0 ms] compared to the no delay condition [0 ms, 0 ms] and a significant decrease in the constant delayed tap [100 ms, 100 ms] compared with the test delay [0 ms, 100 ms]. Further, as a result of the steady increase of initial exposure between experiment two, three, and four, we predict there will be a significant increase in the shift of immediate touch and a significant increase in the shift of the delayed touch between the experiments.

Experiment four: Results

During 0 ms exposure we found significant attenuation of only the immediate test tap [0 ms, 0 ms] (mean PSE = 1.82, SD = 0.14) when compared to the baseline (mean PSE = 1.96, SD = 0.14) using a paired t-test, $t(29) = 4.84$, mean difference = 0.13, 95% confidence interval [CI] = [0.19, 0.08], $p < 0.001$. The delayed tap during exposure to immediate touch [0 ms, 100 ms] (mean PSE = 1.97, SD = 0.11) was not significantly differently from the baseline as tested with a paired Wilcoxon Signed Rank test (Shapiro-Wilk normality test, W = 0.85, $p < 0.001$), V = 248, p = 0.76. As expected from previous experiments, the delayed tap [0 ms, 100 ms] felt significantly more intense than the immediate tap [0 ms, 0 ms] (Shapiro-Wilk normality test W = 0.88, $p < 0.001$) paired Wilcoxon signed rank test, V = 15, $p < 0.001$.

Figure 9. Experiment four results

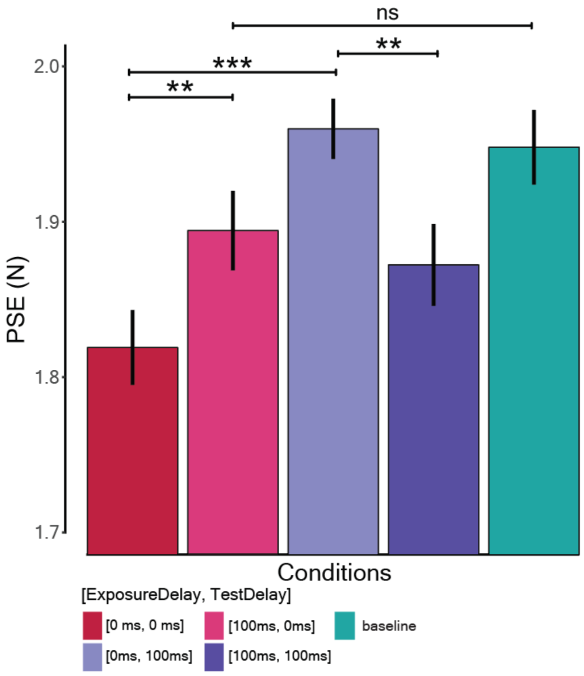

Figure 9. Mean PSE gathered for each condition in experiment four with bars displaying ± standard error. Only important comparisons are displayed (**p < 0.01, *** p < 0.001, ns = not significant). Importantly, participants attenuate the delayed tap after delay exposure.

After exposure to a 100 ms delay participants perception of the intensity of the immediate tap significantly increased [100 ms, 0 ms] (mean PSE = 1.90, SD = 0.15) in comparison to 0 ms delay exposure [0 ms, 0 ms], *t*(29) = 3.03, mean difference = 0.08, 95% Confidence interval [CI] = [0.13, 0.25], p < 0.01. There was only a trend between the immediate tap after delay exposure [100 ms, 0 ms] and the baseline, *t*(29) =1.74, mean difference = 0.06, 95% confidence interval [CI] = [-0.01, 0.12], p = 0.092. This difference from both the immediate touch and the somatosensory baseline suggests participants unlearned to accurately predict the immediate tap.

Figure 10. Shift in attenuation of the immediate test tap

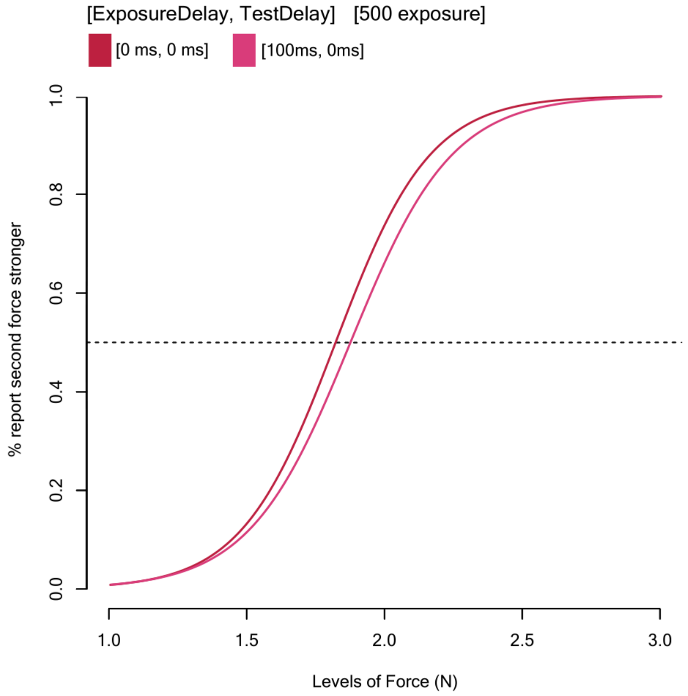

Figure 10. The logistic regressions fitted using the mean PSE and mean JND at 75% of the no delay condition [0 ms, 0 ms] and the exposure delay condition [100 ms, 0 ms]. The shift of the curve towards the right indicates an increase in the perception of the intensity of the test tap between the two conditions, suggesting participants no longer predict the immediate tap after exposure to a 100 ms delay.

Vice versa, participants learned to predict the delayed tap after delay exposure [100 ms, 100 ms] (mean PSE = 1.88, SD = 0.15) as indicated by the significant decrease of the mean PSE compared to the test delay condition [0 ms, 100 ms], *t*(29) = 3.52, mean difference = 0.09, 95% confidence interval [CI] = [0.03, 0.14], p < 0.01. Additionally, the delayed test tap after delay exposure [100 ms, 100 ms] was also significantly different from the baseline, *t*(29) = 2.24, mean difference = 0.08, 95% confidence interval [CI] = [0.007, 0.15], p = 0.03.

Figure 11. Shift in attenuation of the delayed test tap

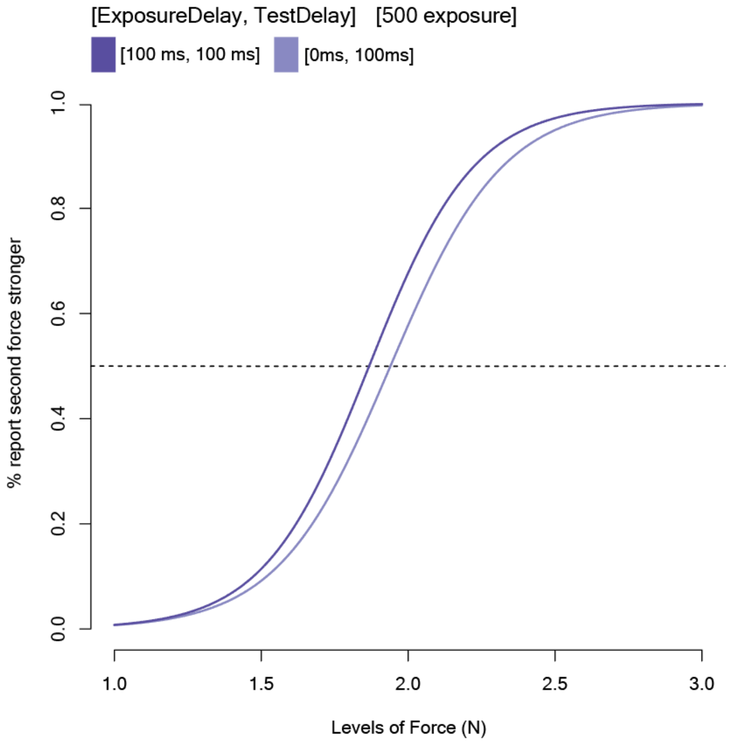

Figure 11. Logistic regressions fitted using the mean PSE and mean JND for the test delay [0 ms, 100 ms] and constant delay [100 ms, 100 ms] conditions. The shift towards the left indicates that participants perceive the delayed tap less intense after delay exposure, meaning that they updated their internal forward model and started to predict the delayed tap.

Interestingly, the degree to which participants learned the delayed tap and unlearned the immediate tap were significantly correlated: Pearson's $r = 0.473$, $t(28)$, p = 2.84, $p < 0.01$. Lending evidence towards the hypothesis that a single internal forward model is updated or recalibrated throughout the task rather than acquiring a new model.

Figure 12. Correlation between learning and unlearning.

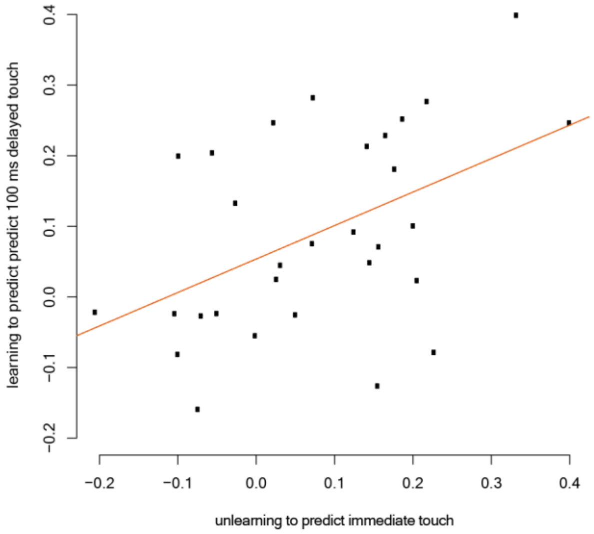

Figure 12. Scatterplot of the shifts in attenuation of the immediate touch (unlearning in the x-axis) and delayed touch (learning in the y-axis). The orange line indicates the fitted linear regression.

We hypothesized that as a result of added exposure between the experimental groups we would see an increased shift in attenuation of the immediate tap and the delayed tap (Figure 12). The shift for the immediate tap is the difference between the no delay [0 ms, 0 ms] and exposure delay [0 ms, 100 ms] conditions. Similarly, attenuation of the delayed tap is the difference between the test delay condition [0 ms, 100 ms] and the constant delay condition [100 ms, 100 ms]. We did Welch Two Sample t-tests between the mean shifts of immediate and delayed touch observed in each experiment.

There were no observed significant differences in the attenuation of the immediate tap between any of the experiments. First, we compared the shift in attenuation of the immediate tap between experiment two (mean shift = 0.04, SD = 0.07) and experiment three (mean shift = 0.06, SD = 0.06), *t*(57.043) = 1.04, 95% confidence interval [CI] = [-0.02, 0.05], p = 0.30. Second, we compared the shift in attenuation between experiment two and experiment four (mean shift = 0.04, SD = 0.07), *t(*57.904) = 0.22, 95% confidence interval [CI] = [-0.03, 0.04], p = 0.83. Lastly, we compared the shift in attenuation between experiment three and experiment four, *t*(56.4) = 0.79, 95%

confidence interval [CI] = [-0.02, 0.05], p = 0.43. There can be several explanations as of why the shift in attenuation of the immediate remained the same across the three experiments regardless of the amount of exposure. One possible reason is that the immediate tap is experienced similar to passive perception of the forces meaning there could be a natural ceiling effect. Once participants unlearn to predict the immediate tap it will not be perceived greater than baseline perception of touch.

Figure 13. Attenuation shifts between experiments

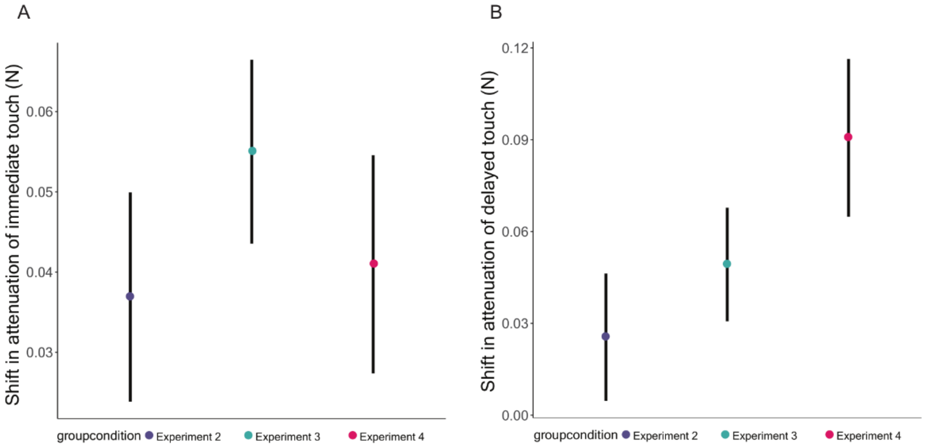

Figure 13. The shift in attenuation between experiments defined as the PSE for each participant in the no delay condition [0 ms, 0 ms] subtracted from the PSE of the exposure delay condition [100 ms, 0 ms] (A). Same type of definition was used for the shift in attenuation of the delayed test tap (B). The shift is defined as the PSE for each participant in the constant delay condition [100 ms, 100 ms] subtracted from the test delay condition [0 ms, 100 ms] (B). There were no differences in shift of the attenuation of the immediate tap as a result of increased exposure (a). However, we did see an interesting increase in the attenuation shift of the delayed tap.

Additionally, we observed no significant shifts in attenuation of the delayed test tap. First, we compared the shift in attenuation between experiment two (mean shift = 0.026, SD = 0.11) and experiment three (mean shift = 0.05, SD = 0.10), *t*(57,26) =

0.85, 95% confidence interval [CI] = [-0.03, 0.08], p = 0.40. Second, we compared the shift between experiment three and experiment four (mean shift = 0.09, SD = 0.14), *t*(52.70) = 1.30, 95% confidence interval [CI] = [-0.02, 0.11], p = 0.20. Finally, we compared the shift in attenuation of delayed touch in experiment two and experiment four, *t*(55.5) = 1.97, 95% confidence interval [CI] = [-0.001, 0.13], p = 0.0543. While we did not observe a significant difference in the shift of attenuation, there was a strong trend between the resulting shift in attenuation of the delayed tap after 50 trials of initial exposure and 500 trials of initial exposure. From these between experiment tests, we cannot definitively conclude that the amount of initial exposure had an effect on the observed shifts in attenuation. However, that we observed an effect in the experiments with increased initial exposure (experiment three and four) compared to experiment two with a limited amount of initial exposure suggests that exposure does in fact affect learning to predict a temporal delay. Returning to the strong trend in learning between experiment two and four, which does suggest that an effect could exist. The question of degree of learning as a function of exposure is perhaps better studied in a within-subject design which holds more statistical power, is more sensitive, and provides considerably less error variance associated with individual differences. This is an avenue for exploration in future experiments.

Discussion

In the present study we investigated if temporal recalibration can be reflected by updating the sensory predictions made by an internal forward model. If this is the case we should observe attenuation of self-generated but delayed touch when participants are exposed to consistent delay. Further, if the parameters of a single existing forward model are updated by incoming evidence in favor of delayed touch, predictions of immediate touch would be abandoned in favor of delayed touch. As it turns out this is indeed the case as indicated by the shifts in attenuation of immediate and delayed touch in opposite facing directions in experiment three and four.

In all four experiments we saw immediate touch was no longer attenuated, thus no longer predicted as a sensory consequence by the forward model. However, only in experiment three and four did we observe significant attenuation of delayed touch. This finding further suggest that predictions of a single forward model are updated rather than acquiring a new model. The asymmetry in findings of learning to predict the delay and unlearning further indicates that different rates of learning and unlearning occur, at a slow rate for the former and at a fast rate during the latter.

In the case of temporal perturbations, it is rather counter-intuitive that we unlearn to expect immediate touch at a quicker rate than we learn to predict delayed touch. Probability estimates based on prior experience should favor immediate touch since we always experience self-generated touch as immediate throughout our lives. Such asymmetry between learning and unlearning has previously been observed and is thought to reflect identification of contextual change (Wolpert & Kawato, 1998, p. 1319). An explanation could be that the mismatch in temporal prediction identifies a new experimental context and participants rapidly learn that the normal instantaneous relationship between action and sensory consequence does not apply and then gradually fine tune their predictions of delayed touch during exposure i.e. a large error signal initially indicates contextual change and the error signal then gradually decreases with learning (ibid.; Wolpert et al., 2011, p. 745). A two-state multi-rate model based on the cerebellar cortex and the cerebellar nuclei has been proposed to further explain observed asymmetries in timescales of learning, unlearning, and relearning as the interaction between a fast and a slow learning process (Smith et al., 2006). We can however only indirectly make this inference based on the results of these experiments. A limit of the forced choice discrimination task used in these experiments is that we cannot observe trial-to-trial adaptation. The PSE only informs us of perceived equivalence between two forces at one point in time over the course of the 70 trials required for fitting the logistic regression. More experiments directly investigating this relationship between unlearning and learning of delays are needed.

These results conclusively demonstrate that when the forward model makes predictions about sensory consequences of movement the temporal relationship is also computed, compared, and updated. The cerebellum has been targeted as a likely candidate where internal inverse and forward models reside (Miall, Weir, Wolpert, & Stein, 1993; Wolpert, Miall, & Kawato, 1998). It has been demonstrated that cerebellum is widely implicated in predictions of self-generated somatosensory consequences (Blakemore, Wolpert, & Frith, 1999b; Blakemore, Frith, & Wolpert, 2001). Further it has also been demonstrated in attenuating the BOLD responses of areas related to visual and auditory stimuli, meaning it not only predicts somatosensory consequences (Straube, et al., 2017). It also has important relevance for time perception and temporal coordination of movements (Ashmore & Sommer, 2013; Ivry & Keele, 1989; Jueptner et al., 1995). More importantly, cerebellum has a well-established role in motor learning demonstrated through lesion, scanning, and transcranial stimulation studies (Wolpert et al, 2011; Smith & Shadmehr, 2005; Tseng, Diedrichsen, Krakauer, Shadmehr, & Bastian, 2007; Galea et al., 2011; Cao et al, 2017; Butcher et al, 2017). It has also been shown how cerebellum activity reflects the acquisition of an internal model for a new tool by a decreasing MR signal thought to be caused by error in prediction (Imamizu et al., 2000). Demonstrating how we acquire a new model and update it when we learn skillful use of a new tool (ibid.). Further, this acquired model for a tool also computes the added mechanical delay of a tool and its associated sensory consequences (Imamizu & Kawato, 2012, p. 334). Several studies have been done on cerebellar activity during spatial perturbation which demonstrate adaptation is cerebellar dependent (Tseng et al, 2007; Smith & Shadmehr, 2005; Butcher et al., 2017). However, an experiment applying single pulse Transcranial Magnetic Stimulation (TMS) over the Posterior-Parietal Cortex (PPC) found that this significantly interfered with learning (Della-Maggiore, Malfait, Ostry, & Paus, 2004). The PPC has been suggested to represent the actual comparator in models of sensory attenuation, which forms the basis for the error-signal, it can monitor spatial and temporal congruence between the motor command and its predicted multisensory consequence (Jeannerod, 2006, p. 83). It has been proposed that initial learning of a skill or a tool is acquired in premotor and parietal area, but with increasing training control becomes rapid and precise in a predictive fashion reminiscent of the processing observed in cerebellum (Imamizu & Kawato, 2012). Studies disrupting the primary motor cortex during learning tasks found no effects on learning, however it does retain a skill once it has been learned (Hadipour-Niktarash, Lee, Desmond & Shadmehr, 2007; Galea et al, 2011). Interestingly, a study applying repetitive TMS over the primary motor cortex during periods of motor memory consolidation did not interfere with memory formation (Baraduc, Lang, Rotwell, & Wolpert, 2004). These findings further support the cerebellum and the premotor-parietal network as primary areas of motor-skill learning and error-based learning.

Learning the temporal statistics of the external world is an important aspect of engaging with the world and also for acquiring and interacting with tools that may have a mechanical delay between the motor command and the expected sensory consequence (Imamizu & Kawato, 2012). It has been demonstrated that we carry internal representations of temporal statistics which can be explained by rules of Bayesian inference, further suggesting a predictive mechanism for sensorimotor timing (Acerbi, Wolpert, & Vijayakumar, 2012). Previous studies measuring the attenuation of activation in relevant sensory areas reveal that this suppression of activity also happen during repetitive and predictable presentation of stimuli and is thought to be predictive (Schafer & Marcus, 1973; Eagleman, 2008, p. 133). Studies on temporal recalibration also reveal shifts in perception of simultaneity as a result of asynchrony between two sensory events (Stetson et al., 2006; Vroomen et al., 2004; Vroomen & Keetels, 2010).

This poses an important question to our results: Is the attenuation we observe a result of error-based motor learning? Or can it be explained by the predictability of tactile feedback between the left and right hand? Is it the time interval between the tactile touch on both hands or do forward models predict an additional time delay between motor action and predicted feedback? We observed that attenuation mostly occurred in conditions of either constant immediate feedback or constant delayed feedback and not in conditions where the test delay differed from the exposure delay, which is not incompatible with such an account of the results. To conclusively test which explanation is the case a control experiment of similar design should be performed. Either by removing afferent sensory information of the right hand producing the movement, in which case one would expect the same shifts we observe if participants update an internal forward model. Or, by performing a cross-sensory recalibration experiment similar to the control experiment of Stetson and colleagues (2006), where we would predict no attenuation of the tap on the left finger after an external tactile touch on a subject’s right finger. Such an experiment has been carried out using discrimination of forces instead of temporal order judgements, the PSE observed was not significantly different from passive somatosensory perception of the forces (Bays et al, 2005). However, our study has many repetitions of this which could possibly produce small attenuation by the sheer amount of times it is repeated. In a lag-adaptation study using inhibitory TMS over cerebellum with a 15-minute 1 Hz repetitive stimulation protocol and MEG measurements of sensory evoked potentials participants triggered sounds by lifting their finger (Cao et al, 2017). The finger lift was detected by a laser, which would then trigger a sound after a short delay of 92 ms (Cao et al., 2017). They find attenuation of evoked potentials in auditory areas within 300 trials as found by other E/MEG studies (Aliu et al., 2009; Elijah et al., 2016). Crucially, there is no significant associated tactile event at the end of the movement which triggers the sound, which lends further support in favor of updating an internal forward model (Cao et al., 2017).

While research on cerebellar contributions to sensorimotor learning has benefitted a lot from designs using force-field, visuomotor, and spatial adaptations, relatively few studies have used similar implementations of lag adaptation. Cerebellar processing has been shown to be highly temporally precise and adapted to operate in fast and precise temporal regime (Sultan et al, 2012, p. 7). This also makes the cerebellum an ideal target for temporal processing. In a study investigating several types of neurological deficits on timing perception and production, they found that only patients with cerebellar dysfunction showed deficiency in rhythmic tapping and differences in stimuli duration (Ivry & Keele, 1989). They argue that a timing mechanism can be conceptualized as an isolable part of the motor system, which predictive computations is employed by perceptual and cognitive systems (ibid).

Cerebellar activity has for example been observed in fMRI during passive perception of the rubber-hand illusion (Ehrsson, Spence, & Passingham, 2004; Ehrsson, Holmes, & Passingham, 2005; Gentile, Guterstam, Brozzoli, & Ehrsson, 2013; Guterstam, Gentile, & Ehrsson, 2013). Reflecting how cerebellar temporal processing generate cross-modal timing predictions which are employed by premotor and intraparietal cortices to judge congruency (Guterstam et al., 2013, p. 1096). It has also been demonstrated to update predictions during sensorimotor learning of a timing delay between action and sensory consequence (Cao et al., 2017). Inhibitory TMS applied to the cerebellum during lag adaptation removed the trial-by-trial suppression of the M100 component of evoked potentials observed in auditory cortex during the sham condition (ibid., p 2447). Further, they find significantly increased attenuation of the M100 component between the first session and the second session which are separated by a 15-minute break (ibid., p. 2446). This is interesting as it could suggest consolidation of implicit motor learning, further strengthening the hypothesis of forward model predictions. Consolidation has been observed to have a considerable effect on learning and later *re*-learning a perturbation after a short break (Krakauer, 2009, p. 3). Cao and colleagues (2017) could reflect anterograde carryover effects of learning to the second session, an expression of off-line learning (Krakauer, 2009, p. 3). While it may suggest that lag adaptation is a motor learning phenomenon, it is meanwhile unclear whether TMS disrupted error-based learning, consolidation of learning, or both. Recently a new computational model which demonstrates how cerebellar learning mechanisms encode and learn prior distributions of time intervals (Narain, Remington, De Zeeuw, Jazayeri, 2018). Further, it confirms that these conform to rules of Bayesian inference and that these estimates can be captured by learning in cerebellar cortex as well as computations in the cerebellar deep nuclei (Acerbi et al., 2012; Narain et al., 2018).

Conclusion

This paper proposes that the observed shifts in attenuation during exposure to a temporal delay reflects a form of motor learning which recalibrates and updates the temporal parameters of the expected relationship between executed action and its sensory consequence. This form of temporal learning, in contrast to motor learning paradigms using force-field perturbations and visuomotor rotations, occurs in a temporal domain. The purpose of this form of learning is to continually adjust temporal dimensions of sensorimotor predictions in order to overcome difficulties of varying delays in sensory feedback processing, changing conditions in our bodies, changes in the environment, the changing nature of tasks, as well as the tools we acquire and use to solve said tasks. Further, it is speculated that this learning is reflected in plastic processes in the cerebellar cortex and the cerebellar deep nuclei, which has been demonstrated to have very temporally precise and rapid processing, ideal for temporal processing.

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