

An electrophysiological investigation into the role of agency and contingency on sensory attenuation

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Thesis/Dissertation Sheet

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Abstract 350 words maximum: (PLEASE TYPE)

Stimuli generated by a person's own willed actions generally elicit a suppressed neurophysiological response than physically identical stimuli that have been externally generated. This phenomenon, known as sensory attenuation, has primarily been studied by comparing the N1, Tb and P2 components of the event-related potentials (ERPs) evoked by self-initiated vs. externally generated sounds. Sensory attenuation has been implicated in some psychotic disorders such as schizophrenia, where symptoms such as auditory hallucinations and delusions of control have been conceptualised as reflecting a difficulty in distinguishing between internally and externally generated stimuli. This thesis employed a novel paradigm across five experiments to investigate the role of agency and contingency in sensory attenuation. The role of agency was investigated in Chapter 2. In Experiment 1, participants watched a moving, marked tickertape while EEG was recorded. In the *active* condition, participants chose whether to press a button by a certain mark on the tickertape. If a button-press had not occurred by the mark, then a tone would be played one second later. If the button was pressed prior to the mark, the tone was not played. In the *passive* condition, participants passively watched the animation, and were informed about whether a tone would be played on each trial. The design for Experiment 2 was identical, except that the contingencies were reversed (i.e., pressing the button prior to the mark led to a tone). The results were consistent across the two experiments: while there were no differences in N1 amplitude between the *active* and *passive* conditions, the amplitude of the Tb component was suppressed in the *active* condition. The amplitude of the P2 component was enhanced in the *active* condition in both Experiments 1 and 2. These results suggest that agency and motor actions *per se* have differential effects on sensory attenuation to sounds and are indexed with different ERP components. In Chapter 3, we investigated the role of contingency in sensory attenuation while using a similar tickertape design in Chapter 2. In the *Full Contingency (FC)* condition, participants again chose whether to press a button by a certain mark on the tickertape. If a button-press had not occurred by the mark, a sound would be played (one second later) 100% of the time (Experiment 3). If the button was pressed prior to the mark, the sound was not played. In the *Half Contingency (HC)* condition, participants observed the same tickertape; however, if participants did not press the button by the mark, a sound would occur 50% of the time (*HC-Inaction*) while if the participant did *press* the button, a sound would also play 50% of the time (*HC-Action*). In Experiment 4, the design was identical, except that a button-press triggered the sound in the *FC* condition. The results were consistent across both Experiments in Chapter 3: while there were no differences in N1 amplitude across the *FC* and *HC* conditions, the amplitude of the Tb component was smaller in the *FC* condition when compared to the *HC-Inaction* condition. The amplitude of the P2 component was also smaller in the *FC* condition compared to both the *HC-Action* and *HC-Inaction* conditions. The results suggest that the effect of contingency on

neurophysiological indices of sensory attenuation may be indexed by the Tb and P2 components, as opposed to the more heavily studied N1 component. Chapter 4 also investigated contingency but instead used a more ‘traditional’ self-stimulation paradigm, in which sounds immediately followed the button-press. In Chapter 4, participants observed a fixation cross while pressing a button to generate a sound. The probability of the sound occurring after the button-press was either 100% (*active 100*) or 50% (*active 50*). In the two *passive* conditions (*passive 100* and *passive 50*), sounds generated in the corresponding *active* conditions were recorded and played back to participants while they passively listened. In contrast with the results of Chapter 3, the results of Chapter 4 showed both the classical N1 suppression effect, and also an effect of contingency of the N1, where sounds with a 50% probability generated higher N1 amplitudes compared to sounds with 100% probability. In contrast, Tb amplitude was modulated by contingency but did not show any differences between the *active* and *passive* conditions. The results of this study suggest that both sense of agency and sensory contingency can influence sensory attenuation, and thus should be considered in future studies investigating this theoretically and clinically important phenomenon.

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Thesis Title

An electrophysiological investigation into the role of agency and contingency on sensory attenuation

Thesis Abstract

Stimuli generated by a person's own willed actions generally elicit a suppressed neurophysiological response than physically identical stimuli that have been externally generated. This phenomenon, known as sensory attenuation, has primarily been studied by comparing the N1, Tb and P2 components of the event-related potentials (ERPs) evoked by self-initiated vs. externally generated sounds. This thesis employed a novel paradigm across five experiments to investigate the role of agency and contingency in sensory attenuation. The role of agency was investigated in Chapter 2. In Experiment 1, participants watched a moving, marked tickertape while EEG was recorded. In the *active* condition, participants chose whether to press a button by a certain mark on the tickertape. If a button-press had not occurred by the mark, then a tone would be played one second later. If the button was pressed prior to the mark, the tone was not played. In the *passive* condition, participants passively watched the animation, and were informed about whether a tone would be played on each trial. The design for Experiment 2 was identical, except that the contingencies were reversed (i.e., pressing the button prior to the mark led to a tone). The results were consistent across the two experiments: while there were no differences in N1 amplitude between the *active* and *passive* conditions, the amplitude of the Tb component was suppressed in the *active* condition. The amplitude of the P2 component was enhanced in the *active* condition in both Experiments 1 and 2. These results suggest that agency and motor actions *per se* have differential effects on sensory attenuation to sounds and are indexed with different ERP components. In Chapter 3, we investigated the role of contingency in sensory attenuation while using a similar ticker-tape design in Chapter 2. In the *Full Contingency (FC)* condition, participants again chose whether to press a button by a certain mark on the tickertape. If a button-press had not occurred by the mark, a sound would be played (one second later) 100% of the time. If the button was pressed prior to the mark, the sound was not played. In the *Half Contingency (HC)* condition, participants observed the same tickertape; however, if participants did not press the button by the mark, a sound would occur 50% of the time (*HC-Inaction*) while if the participant did *press* the button, the a sound would also play 50% of the time (*HC-Action*). In Experiment 2, the design was identical, except that a button-press triggered the sound in the *FC* condition. The results were consistent across both Experiments in Chapter 3: while there were no differences in N1 amplitude across the *FC* and *HC* conditions, the amplitude of the Tb component was smaller in the *FC* condition when compared to the *HC-Inaction* condition. The amplitude of the P2 component was also smaller in the *FC* condition compared to both the *HC-Action* and *HC-Inaction* conditions. The results suggest that the effect of contingency on neurophysiological indices of sensory attenuation may be indexed by the Tb and P2 components, as opposed to the more heavily studied N1 component. Chapter 4 also investigated contingency but instead used a more 'traditional' self-stimulation paradigm, in which sounds immediately followed the button-press. In Chapter 4, participants observed a fixation cross while pressing a button to generate a sound. The probability of the sound occurring after the button-press was either 100% (*active 100*) or 50% (*active 50*). In the two *passive* conditions (*passive 100* and *passive 50*), sounds generated in the corresponding *active* conditions were recorded and played back to participants while they passively listened. In contrast with the results of Chapter 3, the results of Chapter 4 showed both the classical N1 suppression effect, and also an effect of contingency of the N1, where sounds with a 50% probability generated higher N1 amplitudes compared to sounds with 100% probability. In contrast, Tb amplitude was modulated by contingency but did not show any differences between the *active* and *passive* conditions. The results of this study suggest that both sense of agency and sensory contingency can influence sensory attenuation, and thus should be considered in future studies investigating this theoretically and clinically important phenomenon.

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**An electrophysiological investigation into the role of
agency and contingency on sensory attenuation**

Nathan Thomas Han

Primary supervisor: Prof. Thomas J. Whitford

Secondary supervisor: Prof. Mike Le Pelley

A thesis presented for the degree of

Doctor of Philosophy



School of Psychology

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University of New South Wales

September 2021

Abstract

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Chapter 1: General Introduction

How are we able to navigate the world so fluidly? Consider the ‘commonsense’ view of perception and action in which we first process sensory input and then act upon the data. If we take this view as the basis of action, it will necessarily imply that we are always acting one step behind the present. As Franklin and Wolpert (2011, p. 425) described:

“Delays are present in all stages of sensorimotor system, from the delay in receiving afferent sensory information, to the delay in our muscles responding to efferent motor commands. Feedback of sensory information (that we take to include information about the state of the world and consequences of our own actions) is subject to delays arising from receptor dynamics as well as conduction delays along nerve fibers and synaptic relays.”

In order so that we can move in the present, our neurological apparatus relies on prediction to navigate our way through the vast sea of sensory information. This idea of prediction is central to several frameworks that purport to explain how we perceive the world and, by extension, execute smooth motor movements. Examples of such frameworks include the free-energy principle (Friston, 2010; Friston, Daunizeau, Kilner, & Kiebel, 2010), predictive coding (Huang & Rao, 2011), and the Bayesian brain (Knill & Pouget, 2004; Colombo & Seriès, 2012). A common feature of these three frameworks is that they argue the brain attempts to achieve an equilibrium between incoming sensory data and our prior predictions about the outside world. By doing so, we can maximize efficiency with regards to the computational energy necessary to function in our environment. The same principle of prediction is also believed to be the principle that enables us to distinguish the self from the external world. This thesis is concerned with sensory attenuation, which is one mechanism by which we use prediction to distinguish between ‘self’ and ‘other’.

1.1. Sensory attenuation

Sensory attenuation is the phenomenon whereby the perceived intensity of sensations caused by self-generated movements is smaller compared to sensations caused by externally generated movements (Hughes, Desantis, & Waszak, 2013). For example, when walking in a dark alley, people are usually able to ignore their own footsteps, but might be acutely sensitive to the footsteps of another person behind them. The mechanistic basis of sensory attenuation has been argued to involve a duplicate of the motor command being used to predict the sensory consequences of self-generated movements. Sensory attenuation has been conceptualized as a specific example of predictive coding, in which sensory predictions and sensory feedback are compared, and observed deviations (i.e., prediction errors) are used to update and improve the sensory predictions (Crapse & Sommer, 2008; Poulet & Hedwig, 2007; Schütz-Bosbach & Prinz, 2007; Subramanian et al., 2019; Straka, Simmers, & Chagnaud, 2018).

The overarching goal of this thesis is to map out a deeper understanding of the phenomenon of sensory attenuation. Although there is vast literature on this phenomenon, some very significant questions remain unresolved. Two key unresolved questions are the role of *sense of agency*—defined as “*the feeling of control over actions and their [sensory] consequences*” (Moore, 2016)—and the role of *contingency*—defined as the probability of a sensation occurring following an action—in the phenomenon (Hughes et al., 2013; Horváth, 2015). Furthermore, as has been commented on elsewhere (Hughes et al., 2013; Horváth, 2015), there are some limitations to the experimental designs that have been used to investigate sensory attenuation in the existing literature. The experiments described in this thesis represent an attempt to explore the role of *agency* and *contingency* in sensory attenuation, while *concurrently overcoming the aforementioned limitations in experimental design* that have beset much of the sensory attenuation literature. In the section that follows, I

will provide an overview of the existing literature on the sensory attenuation and will introduce the concepts of agency and contingency which will be the primary focus of the thesis.

1.2. Efference copy and corollary discharge

All animals – including, of course, us humans – are faced with the same fundamental question: where does the self end and the external world begin? After all, without some form of intervention, our sensory receptors cannot distinguish between sensory input caused by our own actions and sensory input caused by an external source. If the source of the sensory input remains ambiguous (Crapse & Sommer, 2008), navigation, not to mention survival, becomes an insurmountable issue. For example, in 1823, Charles Bell pondered on the question of why voluntary eye movements did not trigger a person to perceive the visual scene as moving, whereas involuntary movement of the eye (such as when a finger was pressed upon the eye) did (Bell, 1823). He hypothesized that voluntary eye movements elicited extraretinal signals to account for the relative position of objects, whereas involuntary eye movements did not elicit the same signals.

The distinction between these two different types of sensory input was detailed in 1950 by von Holst and Mittelstaedt (von Holst & Mittelstaedt, 1950). Specifically, in their research, they distinguished between “exafference” and “reafference”. Exafference is sensory input that results from the external environment, such as when someone is tickling us. Reafference is sensory input that results from our own movements, an example being the tactile sensations we receive on the feet while walking. A fundamental challenge the brain must overcome, then, is how to differentiate between exafference and reafference, given that sensory receptors are incapable of distinguishing between these two types of sensory input. Without the ability to make this distinction, animals could potentially confuse these two types

of sensory input. For example, as an animal walks, it might not know whether the activation of its skin receptors was due to a predator's paw or due to an inanimate object in its path.

Von Holst and Mittelstaedt (1950) postulated the existence of an “*Efferenzkopie*”, or *efference copy*, in resolving this dilemma. According to this model, to distinguish between these two types of sensory input, the brain makes an efference copy of the outgoing motor command every time an animal performs a willed motor action. This efference copy is used as a basis upon which to make predictions regarding the sensory consequences of the movement (i.e., the reafference). In 1950, a related concept, known as “corollary discharge” (CD), was coined by Sperry (1950). He used the term more generally to detail the motor-related signals that were used to account for the sensory input that resulted from self-generated movements (reafference).

In their review of CD across animal species, Crapse and Sommer (2008) created a taxonomy of higher-order and lower-order CD signaling based on its impact on the nervous system. Lower-order CD processes share a common functionality: namely, sensory filtration and inhibition of sensory input networks that might result in feedback cycles. For example: the nematode worm is an animal that demonstrates the reflex inhibition (Rankin, 1991). It relies on two main reflexes for its avoidance response: forward and backward movements. The nematode moves forward when detecting sensory input at the tail and backwards when detecting sensory input at the head. However, if the nematode were to move forwards, reafference from the sensory receptors at the head would be detected, which would then cause the nematode to move backwards. In the absence of a resolution, the resulting ‘feedback cycle’ should lead to the nematode being unable to move! To resolve this, inhibitory neurons are activated in whenever the nematode moves forward (for example), which act to *suppress* the reafference at the sensory receptors in the head.

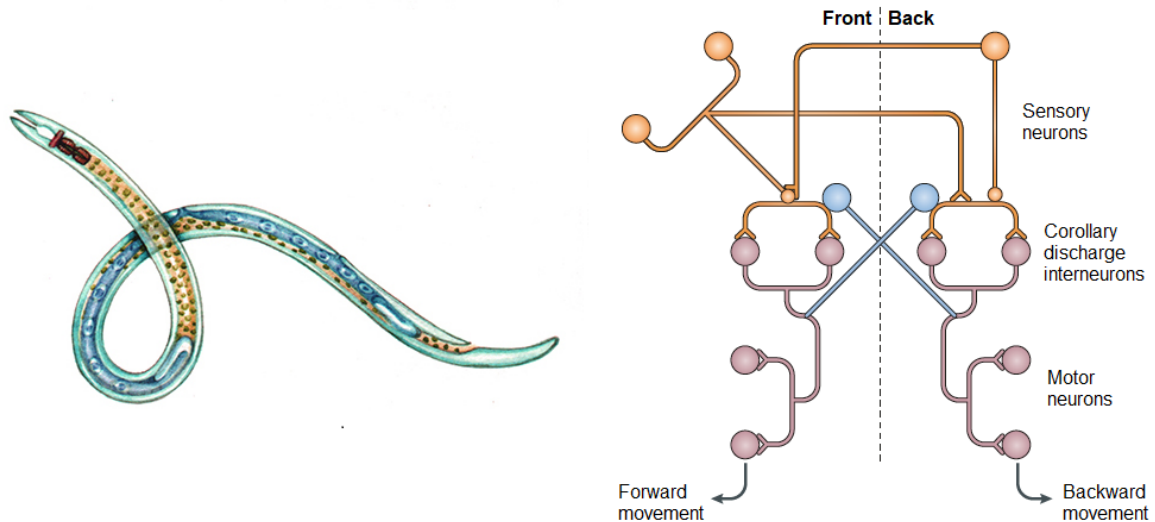


Figure 1. 1. Illustration of a nematode corollary discharge network. The nematode detects sensory input from either the front or the back through its sensory neurons, which elicit movements depending on the direction of sensory input. Interneurons serve corollary discharge functions and help to inhibit the reflex that would otherwise come about as a result of reafference. Adapted from Lizzie Harper Illustrations (2014) and Crapse & Sommer (2008).

A related function of the lower-order CD processes is sensory filtration. For example, the crayfish tail-flips as an escape response to unexpected events (Krasne & Bryan, 1973). Hair-cell mechanoreceptors located on its tail and abdomen monitor signals related to water or air displacement, which are reported to a network of command neurons, triggering the tail-flip. However, one issue that arises during its escape response is that hair cells become repeatedly activated, thus triggering a perpetual cycle of escape responses. CD signals inhibit reafference that result from the initial tail-flip to prevent a feedback cycle of further escape maneuvers.

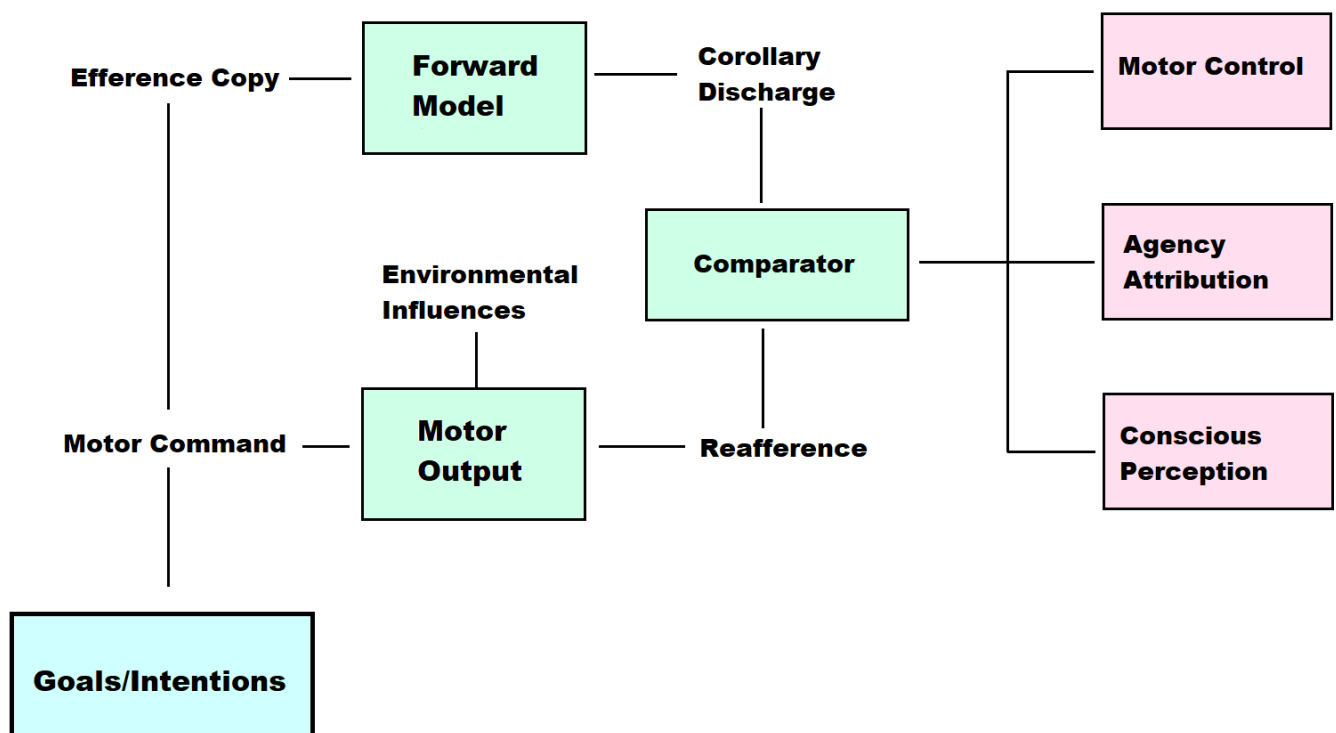
In contrast to lower-order CD, higher-order CD use predictive processes for perception and for the smooth sequencing of consecutive motor actions. For example, bats emit high-intensity, high-frequency sounds and compare the outgoing sounds with the resulting echo to gain information about the surrounding environment (Moss & Sinha, 2003; Neuweiler, 2003). However, the refferent echoes are mixed with noise that originate from

other sources (for example, other bats that emit near-identical noise). To resolve this issue, CDs of vocalisations prime neurons that are sensitive to specific vocal emission-echo time window intervals (Schuller, 1979; Neuweiler, 2003). If the incoming echo occurs within the predicted time-frame, the neurons of that specific emission-echo interval will relay signals containing information about the distance and dimensions of environmental objects for further analysis.

1.3. Sensory attenuation and corollary discharges

The focus of this thesis, sensory attenuation, is one phenomenon that is believed to have its mechanistic underpinnings in CDs. To reiterate, sensory attenuation is the phenomenon where the perceived intensity of sensory consequences resulting from self-generated movements is smaller compared to externally generated movements. Sensory attenuation has long been assumed to result from comparisons between sensory predictions and sensory feedback in *internal forward models* (IFM) (Miall & Wolpert, 1996). When movements are initiated, copies of the outgoing motor command— efference copies— are simultaneously generated. The efference copies are the basis for sensory predictions— the corollary discharge— of the sensory consequences of the self-generated movements. The sensory prediction is then compared to the actual sensory feedback in the so-called ‘comparator’. So far, the cerebellum (Blakemore, Frith, & Wolpert, 2001; Fuentes & Bastian, 2007; Knolle, Schröger, Baess & Kotz, 2011; van Kemenade et al., 2019; Kilteni & Ehrsson, 2020) and parietal cortex (Agnew, McGettigan, Banks, & Scott, 2013; Bansal, Ford, & Ford, 2018) have been implicated as playing a key role in the comparator network. In the basic version of the model, if the sensory prediction does not match that of the actual sensory feedback (reafference), the sensory feedback will be perceived as originating externally. However, if the sensory prediction *does* match that of the actual sensory feedback, the perceived intensity of the sensation is suppressed, and the action is able to be recognized as our own (Blakemore,

Wolpert, & Frith, 2000; Haggard, 2017). The key idea here is that predictive processes – manifested in the form of corollary discharges – help the organism to distinguish between whether a given sensation is self-generated, or whether it has resulted from changes in the external world. In this way, sensory attenuation has also been argued to contribute to our



phenomenological experience of our sense of agency (Hughes et al., 2013; Haggard, 2017).

Figure 1. 2. A schematic representation of the internal forward model. Duplicates of the motor command (called an efference copy) are sent to the internal forward model, which sensory predictions are based upon. Sensory predictions (corollary discharge) are compared to reafference in the comparator and are used in three ways: (1) to fine-tune motor control (2) to attribute agency over actions, and (3) to modulate the conscious perception of actions (sensory attenuation). Adapted from Haggard (2017).

1. 4. Sensory attenuation across the animal kingdom

As previously mentioned, sensory attenuation is a phenomenon that is believed to have its mechanistic underpinnings in CD processes. Much like CD, sensory attenuation has also been demonstrated across multiple species in the animal kingdom. Suga and colleagues (Suga & Schelegel, 1972; Suga & Shimozawa, 1974) have demonstrated that bats across multiple genera show attenuated neural responses to self-vocalised sounds. In an experiment, Suga and Shimozawa (1974) placed electrodes directly to the auditory centres of the bats' brains and recorded neural activity either when (a) bats self-vocalised or (b) a near-identical recording of the vocalisation was played to the bat. The results of their experiment showed that the bats displayed a suppressed neural response to self-vocalisation relative to the neural response to the sound recording, demonstrating sensory attenuation. The mechanism underlying sensory attenuation of vocalizations in bats is believed to involve the middle ear of the bat contracting simultaneously with vocalisation which also helps to attenuate the amount of self-stimulation (Suga & Schelegel, 1972).

More recent research by Eliades and Wang (2003, 2005, 2008) also demonstrated sensory attenuation to self-vocalisations in the marmoset monkey. Like the studies of Suga and colleagues on bats, electrodes were placed into the auditory cortex of the monkeys, and neuronal activity was recorded while monkeys self-vocalised. However, in contrast to these previous studies, in the studies of Eliades and Wang the monkeys did not listen to a recording of their self-vocalisation; instead, the monkeys either heard their unaltered voice or heard their voice that was frequency-shifted ± 2 semitones. Eliades and Wang found that the firing rate of the neurons in the auditory cortex was *suppressed* when monkeys heard their unaltered voice, whereas the firing rate of the same neurons was *increased* when monkeys heard their frequency-shifted voice. The results of their studies demonstrate that sensory predictions have a certain precision; when sensory feedback deviated from what the monkey predicted, the

firing rate of the neurons were no longer suppressed. Referring back to the internal forward model, in the case of self-generated actions, predictions regarding the sensory feedback the organism expects to hear are formulated based on a copy of the motor output. If these predictions are violated (i.e., in the case that the *actual* sensory feedback does not match the *expected* sensory feedback, because it has been pitch-shifted), then it appears that neural activity is no longer suppressed, and may even be amplified. It has been suggested that these deviations between the predicted and actual sensory feedback (i.e., prediction errors) are then used to update and improve future sensory predictions (Houde & Jordan, 1998; Crapse & Sommer, 2008; Poulet & Hedwig, 2007; Schütz-Bosbach & Prinz, 2007; Subramanian et al., 2019; Straka et al., 2018).

1. 5. Sensory attenuation in humans

There are now a substantial number of studies that have demonstrated the phenomenon of sensory attenuation in humans (Blakemore, Wolpert, & Frith, 1998, 2000; Bäß, Jacobsen, & Schröger, 2008; Knolle et al., 2012; Horváth & Burgyán, 2013; SanMiguel, Todd, & Schröger, 2013; Saupe et al., 2013; Elijah, Pelley, & Whitford, 2018; Mifsud et al., 2016; Neszmeélyi & Horváth, 2017; Oestreich et al., 2016; Pinheiro, Schwartz, Gutiérrez, & Kotz, 2019, 2020). An oft-used example of sensory attenuation in humans is the fact that it is difficult to tickle oneself. Tickling represents a clear example where there is a vast gulf in the perceived intensity of the sensation between self-generated and externally generated tickling movements. Tickling as an example of sensory attenuation has been studied extensively by Blakemore and colleagues (Blakemore et al., 1998, 2000). In their experiments, participants controlled a mechanical arm that produced tickling sensations on the palm of their hand. The perceived ticklishness of the sensation was compared to a second condition, wherein the experimenter controlled the same mechanism arm to produce the tickling sensation. The results revealed that participants rated the perceived intensity of the sensation as less ticklish

when the mechanical arm was controlled by themselves (self-generated condition) compared to when the arm was controlled by the experimenter (externally generated condition).

Furthermore, Blakemore et al. (2000) also reported that when they made the sensation less predictable in the self-generated condition (i.e., by introducing a temporal delay between when participants instructed the mechanical arm to move and when it actually triggered the tickling sensation), the perceived intensity of the sensation also increased. Like the study of Eliades and Wang (2008), these results further demonstrated the specificity of the sensory predictions formulated under the IFM.

Blakemore et al. (2000) also conducted a study on the tickling phenomenon but with a schizophrenia population. The study found that participants with symptoms of auditory hallucinations and passivity experiences did not report the same amount of suppression in the perceived intensity of self-generated tickling compared to healthy control participants. This study was one of the first to provide direct empirical support for the hypothesis that patients with schizophrenia suffer from deficits in sensory attenuation, which has been argued to underlie some of the most distinctive symptoms of the disorder (Blakemore et al., 2000; Fletcher & Frith, 2009).

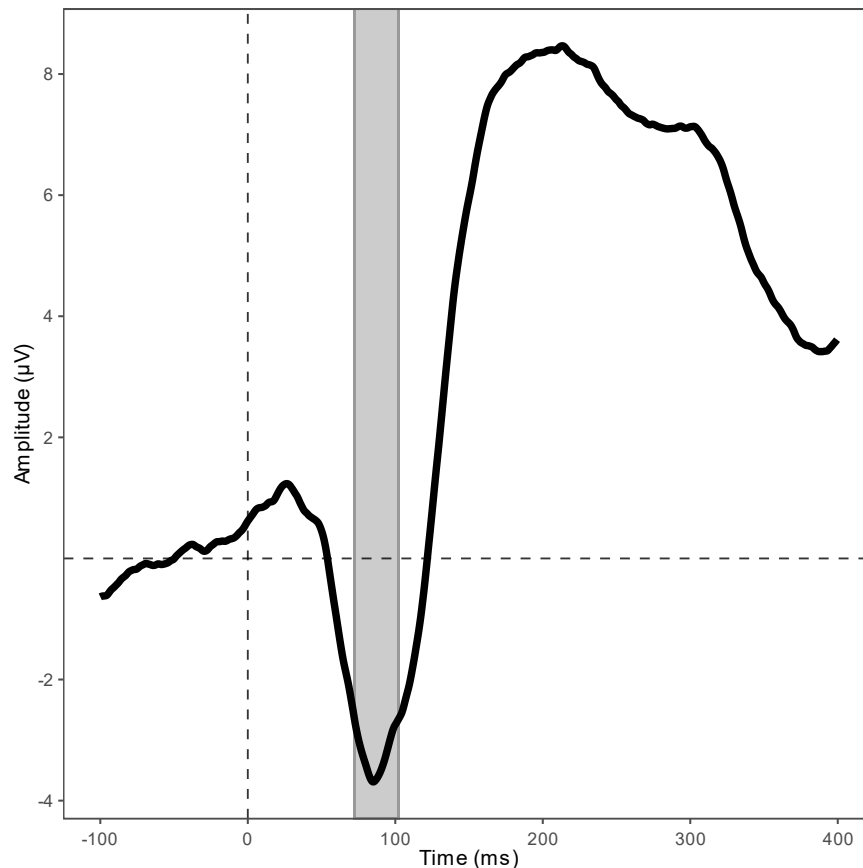
In another sensory attenuation study in the tactile modality, Shergill, Bays, Frith, and Wolpert (2003) investigated force escalation in pairs of healthy participants. Each member of the pair rested their left finger on a molded support and placed their right finger on a lightweight levered torque motor that rested on the other participant's left finger. At the beginning of the experiment, a 0.25 N force was applied to one participant's left finger by the experimenter. The participant was then instructed to reproduce the same level of force on the opposing participant's left finger by pressing on the lever with their right finger. Similarly, the second participant was told to reproduce the same force that the initial participant had applied on them. Despite being explicitly told by the experimenter to reproduce the same

force level, each participant produced a higher force level than they had experienced, thus creating a cycle where participants significantly escalated the amount of force they applied to each other. In short, the self-generated tactile stimuli were perceived as weaker than externally generated stimuli of the same magnitude, which caused participants to overestimate the force necessary to match the other participant. This effect was conceptually replicated in another experiment where a torque motor applied consistent force to a single participant's left finger that was resting on a molded support. Participants were told to reproduce the same level of force as was applied by the motor by using their right finger to push on a force transducer which applied force to their left finger. Here, participants again consistently overestimated the force required; when participants pressed the transducer, the level of force they applied was greater than the actual level of force applied by the motor. Shergill et al. (2003) suggested that the results observed were most likely due to predictive processes (i.e., corollary-discharge-like) that anticipated and attenuated the sensory consequences of the self-generated movement.

1.6. Sensory attenuation in the auditory modality

Apart from the tactile modality, there is also a vast literature showing that sensory attenuation also occurs in the auditory modality in humans (Bäb, Jacobsen, & Schröger, 2008; Knolle et al., 2012; Horváth & Burgyán, 2013; SanMiguel, Todd, & Schröger, 2013; Saupe et al., 2013; Elijah, Pelley, & Whitford, 2018; Neszmélyi & Horváth, 2017; Oestreich et al., 2016). Most of these studies have employed neurophysiological methods such as electroencephalography (EEG) or magnetoencephalography (MEG) (Curio et al., 2000; Bäb, Jacobsen, & Schröger, 2008; Knolle et al., 2012; Horváth & Burgyán, 2013; SanMiguel, Todd, & Schröger, 2013; Saupe et al., 2013; Elijah, Pelley, & Whitford, 2018; Mifsud et al., 2016; Neszmélyi & Horváth, 2017; Oestreich et al., 2016). Most studies using EEG/MEG have focused on the N1 component of the event-related potential (ERP). The N1 component

of the auditory-evoked potential is a negative deflection that generally appears about 50-150 ms after audio stimulus onset (Näätänen & Picton, 1987) (Figure 3), and is believed to be generated in the auditory cortices (Näätänen & Picton, 1987). The N1 is not a unitary component; in contrast, there are believed to be at least three obligatory sources for the N1,



with Components 1 and 2 reflecting sound processing in the primary and secondary auditory cortex, respectively, and Component 3 reflecting reticular processes that facilitate sensory and motor responses to stimuli (Näätänen & Picton, 1987; SanMiguel et al., 2013; Horváth, 2015).

Figure 1. 3. An example of the N1 component of the event-related potential (denoted by the grey window). The N1 component is the first negative deflection occurring at about 100 ms after onset of an auditory stimulus (in this example, the auditory stimulus occurred at time 0 ms).

The amplitude of the N1 component has been shown to index the physical features of sounds, most notably auditory intensity; that is, loud sounds tend to elicit larger N1 amplitudes than soft sounds (Beagley & Knight, 1967; Picton, Goodman, & Bryce, 1970;

Adler & Adler, 1989). To assess sensory attenuation in the auditory modality, N1 amplitude is compared between auditory stimuli that are generated either (i) by the participant themselves (self-generated) or (ii) by some external means (externally generated). If N1 amplitude in the self-generation condition is smaller than N1 amplitude in the external generation condition, this is known as N1-suppression, and has been taken as ostensible evidence of sensory attenuation (Hughes et al., 2013). It is important to mention here that experiments assessing N1 suppression use (or at least *attempt* to use) sounds that are physically identical in both conditions. The fact that N1 amplitude is smaller in the self-generation condition is typically taken to mean that the perceived intensity of the sound is reduced in this condition (Whitford, 2019).

Apart from the N1 component, the experiments in this thesis will also assess the Tb and P2 components within sensory attenuation. Although the sensory attenuation effect has most consistently been found with the N1 component (Bäb, Jacobsen, & Schröger, 2008; Elijah, Pelley, & Whitford, 2018; [Jack et al., 2021](#); Mifsud et al., 2016; Neszmélyi & Horváth, 2017; Oestreich et al., 2016; van Elk et al., 2014; Klaffehn et al., 2019; Pinheiro et al., 2019; Harrison et al., 2021), it has also been identified with the Tb (SanMiguel et al., 2013; Saupe et al., 2013) and P2 components (Knolle et al., 2012; Horváth & Burgyán, 2013).

The Tb is a negative-going component that occurs about 130 – 170 ms after sound onset and is believed to be generated within the secondary auditory cortex (Wolpaw & Penry, 1975; Gallinat et al., 2002; Tonnquist-Uhlen et al., 2003; Rihs et al., 2013), potentially in the vicinity of Wernicke's area (Alain, Woods, & Covarrubias, 1997). While the functional significance of the Tb component has not been definitively established, it has been implicated in auditory processing, particularly of 'high level' auditory stimuli including music and language (Giard et al., 1994; Tonnquist-Uhlen et al., 2003; Shahin, Bosnyak, Trainor, &

Roberts, 2003; Langers, Backes, & van Dijk, 2007; Harpaz, Levkovitz & Lavidor, 2009; Hämäläinen et al., 2011; Bruneau et al., 2003; Azouz et al., 2014).

The P2 is a positive-going component occurs about 150 – 250 ms after sound onset. Several sources are thought to underlie the P2, with one in the PT (planum temporale) and Brodmann Area 22 (the auditory association complex) (Crowley & Colrain, 2004). Although its functional significance is not clear, the P2 component has been associated with attention and categorization processes (García-Larrea, Lukaszewicz, & Mauguière, 1992; Crowley & Colrain, 2004, Lijffijt et al., 2009). Further evidence has also linked the P2 component to working memory processes (Lefebvre et al., 2005; Finnigan et al., 2011; Duzcu et al., 2019).

1. 7. The Talk-Listen experiment

One of the most popular experimental designs for assessing N1 suppression to auditory stimuli is the Talk-Listen experiment (Curio et al., 2000; Ford et al., 2001; Ford & Mathalon, 2004, 2005; Heinks-Maldonado et al., 2005; Ford et al., 2007; Ford, Roach, & Mathalon, 2010). The Talk-Listen experiment resembles the early animal studies, also involving participants producing self-vocalisations. In the prototypical Talk-Listen experiment (see Ford et al., 2010) (Figure 4), participants produce discrete utterances (such as the sound /ah/) every few seconds in the Talk condition and are instructed to listen to a recording of their same self-vocalisations in the Listen condition while EEG is continuously recorded. For example, Curio et al. (2000) conducted a study wherein participants were told to produce self-vocalisations while magnetoencephalography (MEG) was being recorded (Talk condition). The self-vocalisations were recorded, and later replayed to the participant in the Listen condition. The results showed that the M100 (the MEG equivalent of the N1) was suppressed in the Talk condition relative to the Listen condition, suggestive of sensory attenuation of willed speech.

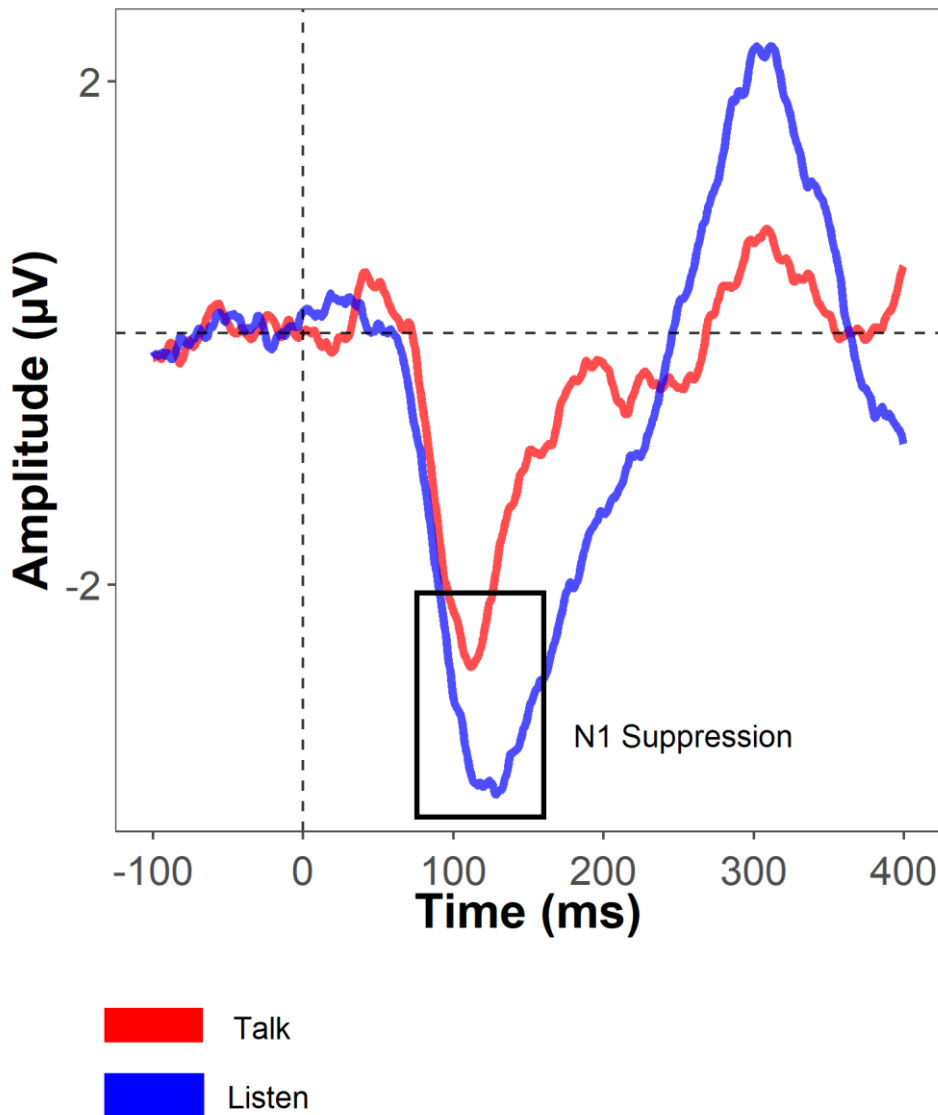


Figure 1. 4. N1 suppression in a traditional Talk-Listen experiment. The ERP generated in the Talk condition is elicited by the participant's self-generated speech, whereas the ERP generated in the Listen condition is elicited by a recording of the participant's self-generated speech. The amplitude of the N1 component in the Talk condition is typically smaller than the amplitude of the N1 component in the Listen condition: this phenomenon is referred to as N1 suppression.

Variations of the Talk-Listen experiment have been carried out to tease out different aspects of the phenomenon of sensory attenuation. Heinks-Maldonado et al. (2005) investigated N1 suppression using a variation of the Talk-Listen experiment in which participants in the self-vocalisation conditions either heard their unaltered voice, their pitch-shifted voice, or an alien voice. Consistent with the pitch-shifting manipulation used by

Eliades and Wang (2008) in their study with macaques, N1 suppression occurred only when the auditory feedback was unaltered in the Talk condition. If the auditory feedback in the Talk condition was altered in some way (e.g., by means of pitch-shifting, or if the feedback was spoken in an alien voice), no N1-suppression was observed. The results of Heinks-Maldonado et al.'s (2005) study suggests that under forward models, predictions about the sensory consequences of a motor action require specificity.

Studies by Ford and colleagues (Ford et al., 2001; Ford & Mathalon, 2004, 2005; Ford et al., 2007) have also used the Talk-Listen experiment to investigate N1-suppression in schizophrenia patients. In Ford et al.'s (2007) study, healthy controls and patients with schizophrenia produced /ah/ vocalisations in the Talk condition and listened to recordings of the same vocalisations in the Listen condition. N1-suppression was compared across the two groups. Whereas healthy controls showed large N1 suppression effects (i.e., significantly larger N1-amplitudes in the Listen relative to the Talk conditions), patients with schizophrenia showed lower levels of N1 suppression. Heinks-Maldonado et al. (2005) also conducted their pitch-shifting version of the Talk-Listen experiment with schizophrenia patients. They found that although healthy controls demonstrated N1 suppression to self-vocalisations but not pitch-shifted or alien substitutions, schizophrenia patients did not show N1 suppression even with their unaltered self-vocalisations. Taken together, the results of these studies (see also Ford et al., 2001; Ford & Mathalon, 2004, 2005; Ford et al., 2007) are consistent with the behavioural results of the tickling studies of Blakemore et al. (2000) and suggest that schizophrenia patients may have a deficit in sensory attenuation processes relative to healthy controls.

To summarize, the collective results of the Talk-Listen studies lend support for the idea that sensory attenuation arises from an internal forward model. However, it must be noted that the Talk-Listen paradigm has some significant methodological limitations/

complications. The first limitation of the Talk-Listen experiment is that in the Talk condition, participants vocalise to produce sounds, resulting in bone conduction to the inner ear (Ford et al., 2010) as well as a contraction of ear muscles for auditory attenuation (Teig, 1973). These factors are not present in the Listen condition (as participants do not have to perform jaw movements in this condition), thus raising a potential confound. Furthermore, because of the (often quite severe) motor artefacts in the EEG induced by vocalisation, experiments using the Talk-Listen experiment have often been required to employ quite strong low- and high-pass filtering of the EEG signal (Ford et al., 2001; Ford & Mathalon, 2004, 2005; Heinks-Maldonado et al., 2005; Ford et al., 2007). Using such strong filters can have major effects on data quality, which can even result in artifactual effects in some circumstances (Kappenman & Luck, 2010; Vanrullen, 2011; Rousselet, 2012; Tanner, Morgan-Short, & Luck, 2015). Partly because of these limitations, many researchers have started exploring the phenomenon of sensory attenuation using other experimental protocols. In the section below, I will discuss what is probably the most used paradigm for exploring sensory attenuation in the auditory domain: the self-stimulation paradigm.

1. 8. The self-stimulation paradigm

The methodological challenges associated with the Talk-Listen paradigm have led researchers investigating sensory attenuation to adopt a paradigm originally developed by Schafer and Marcus (1973), which has been dubbed the self-stimulation paradigm. The self-stimulation paradigm overcomes some of the methodological challenges associated with the Talk-Listen paradigm. In its most basic form, the self-stimulation paradigm consists of two conditions: the *motor-auditory* condition and the *auditory* condition. In the *motor-auditory* condition, participants are required to press a button at will to generate a sound (typically a pure tone). The *motor-auditory* condition is the equivalent of the ‘Talk’ condition in the Talk-Listen task but has the advantage that it is not affected by complications such as bone

conduction and muscle contraction (although, as we shall soon see, it does come with its own set of issues). In the *auditory* condition, participants passively listen to the same series of sounds that were generated in the *motor-auditory* condition. The original experiment by Schafer and Marcus (1973) involved participants pressing randomly on a handheld microswitch to deliver an 80-db click sound (*motor-auditory* condition). In the second *auditory* condition, a tape recorder played back the same sequence of clicks that the participants generated in the *motor-auditory* condition. They also ran a second comparison where visual flashes substituted for the clicks. In both comparisons, they found electrophysiological suppression, with suppression of the N1 component of the auditory-evoked potential and suppression across the vertex area for visual stimuli (although the paper does not seem to mention the individual ERP components for visual stimuli), though the effect was more pronounced with the auditory stimuli. Following on from this original study, there is now a robust literature that has demonstrated N1 suppression with the self-stimulation task (Bäß, Jacobsen, & Schröger, 2008; Knolle et al., 2012; Horváth & Burgyán, 2013; Hughes et al., 2013; SanMiguel et al., 2013; Saupe et al., 2013; Timm, SanMiguel, Saupe, & Schröger, 2013; Timm, Schönwiesner, SanMiguel, & Schröger, 2014; Oestreich et al., 2016; Neszmélyi & Horváth, 2017; Elijah, Pelley, & Whitford, 2018; Pinheiro, Schwartze, Gutiérrez, & Kotz, 2019, 2020; Seidel, Ghio, Studer, & Bellebaum, 2021).

1. 9. Limitations of the self-stimulation paradigm

Notwithstanding its popularity as a measure of sensory attenuation in the auditory domain, the self-stimulation paradigm retains several potential confounds.

1. 9. 1. Motor-evoked potentials

The first of these issues relates to motor-evoked potentials. Although perhaps not as significant a confound as the issues relating to bone conduction and muscle contractions in the Talk-Listen paradigm, the self-stimulation paradigm also requires a motor movement

(typically a finger movement or button-press), which elicits a corresponding motor-evoked potential. Given that the *motor-auditory* condition contains a motor movement while the *auditory* condition does not, it is possible that the motor-evoked potentials can contaminate the EEG signal and contribute to the systematic differences observed between the conditions. Most recent studies using the self-stimulation paradigm have attempted to address this issue by including a third *motor* condition in addition to the other two conditions (i.e., *motor-auditory* and *auditory*) (Bäß et al., 2008; SanMiguel et al., 2013; Neszmélyi & Horváth, 2017; Klaffehn, Baess, Kunde, & Pfister, 2019; Pinheiro, Schwartz, Gutierrez, & Kotz, 2019). In the *motor* condition, participants are told to perform the same motor action that they did in the *motor-auditory* condition except that – in contrast to the *motor-auditory* condition – the motor action does not result in a sound. Instead, the motor-evoked potential elicited from the *motor* condition is typically subtracted from the *motor-auditory* ERP, thus ostensibly creating a ‘motor-corrected’ ERP that can be more freely compared to the ERP in the *auditory* condition.

Until recently, it was widely assumed that the inclusion of *motor* condition was a suitable solution to the issue of motor-related artefact in the *motor-auditory* condition. However, the work of Neszmélyi and Horváth (2017, 2018, 2019; Horváth, 2014, 2015) have argued that this assumption is problematic. Horváth (2014) argued that actions such as the button press in the *motor* condition also produce sounds in and of itself (for example, if one is using a keyboard). This implies that the mechanical impact of pressing the button will also generate auditory ERPs, meaning that the subtraction of the *motor* condition ERP includes not only the motor-evoked potential but also an auditory-evoked potential. Another issue is that of ‘overcompensation’. Neszmélyi and Horváth (2017) conducted a study that assessed the force with which participants engaged in motor actions in the *motor* and *motor-auditory* conditions. Instead of a button press, participants were required to apply force impulses on a

force-sensitive resistor, which could record the physical force that participants applied in each condition. What they found was that participants tended to apply more force in the *motor* condition compared to the *motor-auditory* condition. The authors argued that this was because in the *motor-auditory* condition, participants received confirmation that they performed the motor movement correctly, in the form of a sound following the (correctly performed) motor action. Because there was no such confirmation in the *motor* condition, participants instead overcompensated by using more force to ensure they had performed the movement correctly. If this overcompensation occurred systematically across experiments, it might mean that the motor component in the *motor-auditory* and *motor* ERPs are not equivalent, which would affect the validity of the ‘subtraction’ procedure. Finally, the authors also pointed out that under ideomotor theory (Greenwald, 1970; Pfister, Kiesel, & Melcher, 2010; Shin, Proctor, & Capaldi, 2010), action-effects have a bidirectional relationship. That is, sensory effects are not simply the result of motor actions, but also inform the selection of appropriate motor commands, and thus may have considerable influence on the parameters of motor planning. Consequently, the removal or addition of sensory feedback may affect how motor actions are planned and executed.

1. 9. 2. Temporal predictability

Another potential confound in the self-stimulation paradigm relates to the issue of temporal predictability. In their review paper, Hughes et al. (2013) describe temporal predictability as, “*the ability to predict the point in time at which a sensory event will occur*”. Ideally, the temporal predictability of the sounds in the *motor-auditory* and *auditory* conditions should be equal. This is because N1 amplitude, in addition to being affected by sound intensity (Beagley & Knight, 1967; Picton, Goodman, & Bryce, 1970; Adler & Adler, 1989), is also known to be affected by the predictability (or ‘surprising-ness’) of the sound (Schafer, Amochaev, & Russell, 1981; Bendixen, SanMiguel, & Schröger, 2012; SanMiguel

et al., 2013; Timm et al., 2013). Under the predictive coding account of perception, neuronal responses to stimuli have been argued to reflect prediction errors (Friston, 2005). It has been shown that stimuli that are more temporally predictable trigger smaller neuronal responses than temporally unpredictable stimuli, ostensibly because they result in smaller prediction errors (Schafer et al., 1981; Bendixen et al., 2012; SanMiguel et al., 2013; Timm et al., 2013). Despite this, and problematically (as noted by Hughes et al. (2013)), most sensory attenuation studies in the literature have *not* controlled for the temporal predictability of the sounds. In most previous studies, the auditory stimuli in the *motor-auditory* condition were more predictable than the auditory stimuli in the *auditory* condition. The reason for this is as follows: participants in the *motor-auditory* condition press a button to generate a sound, meaning that they have prior knowledge of when a sound will occur (i.e., because they are responsible for performing the willed action that elicited it). On the other hand, in the *auditory* condition, most previous studies have simply replayed the same sequence of sounds that the participant generated in the *motor-auditory* condition. The upshot of this is that sounds in the *auditory* condition are generally not as predictable as they are in the *motor-auditory* condition. These between-condition differences in temporal predictability could potentially results in artifactual results, particularly given the finding that N1 amplitude is reduced when the timing can be accurately predicted compared to when it cannot with externally generated stimuli (Rothman, Davis, & Hay, 1970; Roth, Ford, Lewis, & Kopell, 1976; Schafer et al., 1981; Clementz, Barber, & Dzau, 2002; Lange, 2009).

Several previous studies have attempted to control for this issue of temporal predictability in the self-stimulation paradigm. One example is a study conducted by Lange (2011). Rather than simply replaying sounds to participants, her study used visual cues to allow for temporal prediction of incoming sounds. In the *self-generation* (button-press) condition, participants were instructed to press a button approximately every two seconds to

generate a sound. In the *visual cue* condition, sounds were presented after a visual cue, with cue-sound contingencies that were either predictable or unpredictable, segregated into different blocks. In the predictable blocks, sounds followed button-presses and visual cues after a fixed delay of either 350 ms or 750 ms (the 350 ms and 750 ms were in separate blocks). In the unpredictable blocks, sounds followed button presses and visual cues after a variable delay of 150 ms, 350 ms, 550 ms, 750 ms, or 950 ms. The results of Lange's (2011) study revealed that N1 amplitudes were smaller when sounds were self-generated compared to the sounds were preceded by a visual cue, regardless of whether the cue was predictive or non-predictive of the sound. These results suggests that the phenomenon of N1 suppression may not be due to between-condition differences in temporal predictability, as the effect remained the same whether self-generation vs visual cueing occurred in predictable or unpredictable blocks.

Bäb et al. (2008) investigated the effect of predictability in terms of the physical (i.e., frequency) and temporal (i.e., onset) properties of the sound in the self-stimulation paradigm. Bäb et al. (2008) used a 2x2 design, with the frequency of the sound being fixed/predictable vs. variable/unpredictable, and the temporal onset of the sound being fixed/predictable vs. variable/unpredictable. In terms of frequency, a predictable sound was a 1000 Hz sinusoidal tone vs. 400 – 1990 Hz for an unpredictable sound. For temporal onset, predictable sounds immediately followed button-presses, whereas unpredictable sounds included a delay of 500 – 1000 ms between the button-press and resulting sound. They included three conditions: the *motor-auditory*, *auditory*, and *motor* conditions. In the *motor-auditory* condition, participants were instructed to generate sounds every 3.5 s by means of a button press. In the *auditory* condition, participants listened to a replay of the sequence of sounds they generated in the *motor-auditory* condition. In the *motor* condition, participants were asked to perform button presses at approximately the same rate as they did in the *motor-auditory* condition. They

found that N1 suppression occurred regardless of whether the pitch or temporal onset of the sound was predictable, although the size of the attenuation effect was largest when stimuli frequency was predictable. A surprising result was that the size of the attenuation effect was smaller when temporal onset was predictable compared to when temporal onset was unpredictable. The results of the study suggested that internal forward models contain dynamic mechanisms that can account for uncertainties in temporal and frequency predictabilities, perhaps contradicting some of the earlier studies suggesting the precise nature of sensory predictions.

While these previous studies have provided important insights into the role of temporal predictability in the sensory attenuation effect, there remain several unresolved issues. For example, Lange's (2011) study found that self-generated sounds elicited smaller N1 amplitudes than externally generated sounds, even when the externally generated sounds were preceded by a visual cue and thus made temporally predictable. However, her study did not allow for conclusions to be made about the precise nature of the difference between self-generated vs. externally generated (visually cued) sounds as the difference between the two types of sounds could have been driven primarily by efference copies leading to a suppression to the neurophysiological response to self-generated sounds or by an enhanced neurophysiological response to sounds that were visually cued. In Bäß et al.'s (2008) study, the 'predictability' of sounds was operationalized by having sounds either immediately follow motor actions (predictable) or after a variable delay (unpredictable). One potential consequence is that the observed N1 suppression may be an effect of the different delays in action-effect contingencies, rather than an effect of temporal predictability *per se*.

The study by Klaffehn et al. (2019) is perhaps one of the best controlled studies that has investigated the effect of temporal predictability on sensory attenuation. This study used an experimental method closely resembling that used in the current thesis. In their Self-Delay

condition, participants pressed a button to generate a sound. However, there was a delay of 750 ms between the button press and sound onset. A loading bar was presented during the 750 ms delay that filled up over the entirety of the 750 ms delay period. The sound was played at precisely the moment when the ‘loading bar’ reached capacity. In the External-Delay condition, sounds were generated at random intervals of 2 – 3 s; however, the loading bar was also presented 750 ms prior to the onset of each sound. The two conditions were set so that the timing of auditory stimuli was equally predictable across conditions. Klaffehn et al. (2019) found that N1 suppression occurred for two of the three electrodes that were measured. The results here suggest that the sensory attenuation effect may persist even when between-condition differences in the temporal predictability of the stimuli are controlled for.

In contrast to the results of Klaffehn et al. (2019), Kaiser and Schütz-Bosbach (2018) found N1 *enhancement* in their results; that is, they found larger N1 amplitudes for self-generated sounds when sounds were equally predictable across all the conditions. They conducted a study wherein a predictive cue was used to make sounds equally temporally predictable across conditions. In their experiment, all sounds, whether self- or externally generated, were preceded by a visual countdown from 3 to 1 (each number stayed on the screen for 500 ms). The countdown was followed by an “X” which served as an indication either for the participant to perform the button-press, with sounds following the button-press (in the *motor-auditory* condition), or as a cue for the sound (in the *auditory* condition). They also included a third *motor* condition to control for motor-evoked potentials. For the *auditory* condition, the timing for sound onset after the appearance of the “X” was directly taken from the time it took for participants to press the button after the “X” appearance in the *motor-auditory* condition. This also allowed for the inter-stimulus interval to be controlled for. Done this way, sounds became equally predictable across all the conditions. Surprisingly, rather than N1 suppression, Kaiser and Schütz-Bosbach found N1 *enhancement* in the experiment.

That is, self-generated sounds elicited larger N1 amplitudes than externally generated sounds. One possible issue of the study, however, is that sounds in the *auditory* condition were perhaps still less predictable than sounds in the *motor-auditory* condition. Sounds in the *motor-auditory* condition could be predicted based on when the participant presses the button. In the *auditory* condition, however, there was a small temporal window following the appearance of the “X” where the participant cannot precisely predict when the sound will appear.

1. 10. Unexplored aspects of sensory attenuation

The issues described so far— motor-evoked potentials and temporal predictability— have been widely discussed in the sensory attenuation literature (e.g., see Hughes et al., 2013; Horváth, 2014, 2015; Neszmélyi & Horváth, 2017, 2018, 2019; Klaffehn et al., 2019). However, there are two additional factors that have been largely neglected in the sensory attenuation literature. These two factors relate to *agency* and *contingency*. Exploring the influence that these two factors have on the sensory attenuation affect will be the primary focus of the thesis.

1. 10. 1. Issues in conceptualizing agency

One aspect of the sensory attenuation phenomenon that has perhaps, to date, been underappreciated is the role of sense of agency. Here, we simply define sense of agency as “*the feeling of control over actions and their [sensory] consequences*” (Moore, 2016). Perhaps owing to its foundational nature, the role of sense of agency has received little attention in the sensory attenuation literature. Like all scientific phenomena, the sense of agency is a construct that must be quantified if it is to be manipulated and its effects measured. Many experiments have used explicit measures to quantify an individual’s sense of agency. These involve simply asking the participant to rate or attribute some outcome to a particular agent; that is, participants must decide the degree to which an outcome was caused

by a particular person. For example, Sato and Yasuda (2005) asked participants to elicit tones via a button-press using either their left or right fingers. These two distinct finger movements produced different corresponding tones, and the association between finger and tone was learned during a training session. Action-effect contingencies were then manipulated so that sounds sometimes violated learned action-effect associations (e.g., a left finger press, which usually resulted in a high-pitched tone, sometimes resulted in a low-pitched tone) or were temporally delayed relative to the button-press. Sato and Yasuda (2005) operationalised sense of agency by asking their participants to rate from 0 (“totally disagree”) to 100 (“totally agree”) how much they agreed with the statement, “I was the one who produced the tone”. Their results showed that incongruent action-effect contingencies caused participants to attribute less agency to themselves. Inserting a temporal delay between the button-press and tone also caused lower agency ratings.

One other method of explicitly assessing agency is through agency attribution. For example, in a study that examined patient apraxia (which can be broadly defined as a disturbance distinct from paralysis that affects a patient’s ability to voluntarily produce motor actions (Pearce, 2009)), Sirigu, Daprati, Pradat- Diehl, Franck, and Jeannerod (1999) instructed apraxic patients and healthy controls to execute specific hand movements while simultaneously receiving video feedback. The video feedback presented either the participant’s hand or an experimenter’s hand, which was performing either a congruent or incongruent hand movement to the one being produced. When the video feedback showed the experimenter performing an incongruent movement from the apraxic patient (*incongruent* condition), patients were able to accurately identify who it was that performed the hand movement on video. However, when the hand on the video screen performed the same movement as the patient (*congruent* condition), apraxic patients were significantly more likely than controls to attribute agency to themselves (that is, they incorrectly identified the

experimenter's hand on the video as their own). This was true even in the case where apraxic patients were *unable* to correctly perform the hand movement shown on the video. In other words, when apraxic patients were instructed to perform a particular gesture and failed to do so, they erroneously attributed the hand movement on the video feedback to be the result of their own hand movement. The results of Sirigu et al. (1999) illustrate that explicit measures of agency can be unreliable; that is, participants can be induced to attribute agency erroneously. Schizophrenia patients are another population where explicit measures of agency can be unreliable (Maeda et al., 2013). In a similar study to that by Sirigu et al. (1999), Daprati et al. (1997) found that compared to healthy controls, schizophrenia patients (and especially those with delusions of control, who have a tendency to misattribute self-generated movements to external agents) were more likely to attribute agency of congruent hand movements incorrectly in a way similar to apraxic patients.

Errors in agency attribution when using explicit measures of agency are not confined to pathological populations. Tsakiris, Haggard, Franck, Mainy, and Sirigu (2005) conducted a similar study to the aforementioned two studies but in a sample of healthy control participants. In their version, participants rested their right-hand index finger on the end of a lever. The lever could be pressed either by the participant's left index finger (self-generated action) or by the experimenter (externally generated action). The visual feedback was manipulated so that participants either saw their own right hand (own hand condition) or someone else's right hand (other hand condition), with the finger on the screen extending because of the lever press. Participants had to judge whether the hand on the video feedback was their own hand or someone else's after the lever press. The results of the experiment showed that when the lever was pressed by the experimenter rather than the participant, participants made significantly more errors in hand attribution relative to when they pressed

the lever themselves, i.e., they tended to incorrectly report that the finger on the screen was their own finger.

These limitations in explicit measures of agency have prompted some researchers to implement more implicit measures of agency. The first of these implicit measures is known as intentional binding. Intentional binding is a phenomenon where a voluntary action (such as a button-press) and its subsequent sensory effect (such as a tone/sound) are perceived to be more temporally compressed compared to involuntary actions (for example, an unwilled motor action triggered by transcranial magnetic stimulation; TMS) (Haggard, Clark, & Kalogeras, 2002; Haggard & Clark, 2003; Moore et al., 2010). ‘Temporally compressed’ here means that participants tended to perceive actions and resulting sounds to be closer in time than they actually were in reality. In the first study to describe the phenomenon, Haggard et al. (2002) had participants voluntarily press a button to trigger a sound while observing a marked clock face, in what was known as the *voluntary action condition*. In the *TMS-induced, involuntary condition*, involuntary presses of the same button were induced via TMS, which caused participants’ hands to twitch involuntarily and consequently press the button. The TMS also produced an audible click when activated. In the *voluntary action condition*, participants were instructed to estimate two specific points in time based on the position of the clockface: (1) the time that they actually pressed the button; and (2) the time at which they heard the sound. In the *TMS-induced, involuntary condition*, participants estimated the time of the audible click and the resulting sound onset. The results of the experiment showed that in the *voluntary action condition*, participants estimated the voluntary button-press to occur later than it actually did, and the resulting sound to occur earlier than it actually did; participants thus perceived the button-press and sound to be closer in time than they actually were in reality. This effect was reversed when the sound was produced via involuntary TMS-induced hand movements- that is, participants estimated the

gap between button-press and sound to be larger when hand movements were induced by TMS and thus involuntary. The intentional binding effect has been widely studied, and the effect has now been replicated several times (Haggard, Clark, & Kalogeras, 2002; Haggard & Clark, 2003; Moore et al., 2010).

A second implicit measure of agency is sensory attenuation, which is the primary topic of this thesis. As discussed previously, suppression of the N1 component by voluntary actions has been considered as another implicit marker of an agent's sense of agency (Haggard, 2017). While comparator models such as the internal forward model were originally used to explain motor control, they have also been used as a model to explain the sense of agency people experience over sensations caused by their own actions (Gentsch & Schütz-Bosbach, 2011). The basic logic behind this argument is as follows: given that N1 suppression is thought to arise from comparator-related processes, and comparator processes are, in turn, thought to be linked to the sense of agency (Carruthers, 2012), then N1 suppression should also be linked to sense of agency. However, to date, very few studies have explicitly investigated the association between sense of agency and sensory attenuation. Furthermore, because of the numerous issues associated with the self-stimulation paradigm (such as those relating to temporal predictability and motor-evoked potentials, as discussed previously), the precise mechanisms that underlie this phenomenon are not clear. For example, as Hughes et al. (2013) notes, deficits in N1 suppression have been interpreted as evidence of aberrant sense in agency for patients with schizophrenia (Ford et al., 2001; Ford & Mathalon, 2004, 2005; Ford et al., 2007). If the sensory attenuation effect is not, in fact, driven by the internal forward model, but rather by between-condition differences in temporal predictability (for example), then the deficits in N1 suppression that have been observed in schizophrenia populations may be indicative of deficiencies in, say, attention, as opposed to

issues in agency attribution. The first two experiments in my thesis will be dedicated to investigating the relationship between agency and sensory attenuation.

1. 10. 2. Contingency

Another area in the sensory attenuation literature that has been relatively sparsely researched is the effect of action-effect contingency on the phenomenon (Horváth, 2015). Here, when I refer to action-effect contingency, I mean the probability that a sensation or stimulus will occur, at a certain predicted time, as a result of a motor action. For example, most action-effect contingencies in the sensory attenuation literature have involved button-presses that cause a sound to be played 100% of the time (Horváth, 2015). To date, there have been several studies that have manipulated action-effect contingencies by manipulating the delay between action and effect (Bäß et al., 2008; Whitford et al., 2011; Timm, et al., 2016; Elijah et al., 2016; Oestreich et al., 2016; Pinheiro et al., 2019). Elijah et al. (2016) conducted an experiment where the temporal delay between actions and the resulting sound were manipulated, and participants were trained to acclimate to the temporal delays. In the real world, sensations typically follow more-or-less immediately from our actions (i.e., with a negligible temporal delay between sensation and action). The question remains open, however, as to whether this ‘prior’ belief is an inherent (‘hardwired’) part of our disposition or whether it is trained by extensive experience. In the experiment by Elijah et al., (2016), the temporal delay between an action and the resulting sound (i.e., the action-effect contingencies) were either 0 ms (immediate sound) or 100 ms (delayed sounds). The experiment contained three main phases: a pre-training phase, a training phase, and a post-training phase. During the pre-training phase, participants were instructed to perform regular button presses. These button-presses resulted in sounds being played either immediately after the button press (immediate sound), or 100 ms after the button press (delayed sounds). In the middle training phase, participants underwent prolonged training to either immediate sounds

or delayed sounds (depending on their group). Participants were again exposed to immediate and delayed sounds at the final post-training phase. The results were as follows: during the pre-training phase, delayed sounds elicited significantly larger N1 amplitudes than undelayed sounds. However, this difference was eliminated at post-training if participants underwent training for delayed sounds in the training phase. The significance of this result is that it demonstrated that expectations regarding the temporal onset of self-initiated sensations can be trained and acclimated for. This would suggest that action-effect contingencies are flexible, to some extent at least.

As just mentioned, most studies that have manipulated contingency in the context of sensory attenuation have done so by inserting a temporal delay between the motor action and the sensory outcome. However, a different way of manipulating action-effect contingency is by varying the probability of the sensory outcome occurring as a result of the motor action. As Horváth (2015) pointed out, most studies using the self-stimulation paradigm have used contingencies of either 100% (i.e., sounds follow the action 100% of the time, such as typically occurs in the *motor-auditory* condition of the self-stimulation paradigm) or 0% (i.e., sounds follow the action 0% of the time, such as typically occurs in the *motor* condition of the self-stimulation paradigm). To my knowledge, no studies in the sensory attenuation literature have manipulated the probability in which action-effect contingencies occur; that is, that have been no studies in the sensory attenuation literature that have manipulated probabilities in such a way so that an action results in a sound only 50% of the time. In the present thesis, investigating the relationship between action-effect contingencies and the sensory attenuation effect is the primary aim of Experiments 3-5.

1. 11. General approach of the experimental paradigm

The experimental paradigm that I developed for this thesis is adapted from the paradigm developed by Whitford et al. (2017) and Jack et al. (2019) to study sensory attenuation in the context of inner speech production. The purpose of using this paradigm is to study the sensory attenuation phenomenon (and specifically the influence of sense of agency and action-effect contingency on the phenomenon) while minimizing the confounds that have been present in much of the existing sensory attenuation literature (such as motor-evoked potentials and temporal predictability). In Whitford et al.'s (2017) experiment, participants observed a visual stimulus that closely resembling a moving tickertape (see Figure 5). In the centre of the tickertape was a fixed line that did not move throughout the duration of the trial (the fixation line). On each trial, a line from the rightmost of the stimulus (called the target line) moved towards the fixation line until they intersected. Participants were instructed to fixate on the fixation line throughout the trial. In these two studies, when the two lines intersected, participants were told to silently produce one of two phonemes in their minds (akin to the *motor-auditory* condition in the sensory attenuation literature), or to passively listen to a recording of the same phonemes (akin to *the auditory* condition in the sensory attenuation literature). When participants silently produced one of the two phonemes in the minds, they simultaneously heard an audible vocalization; the vocalization was of a phoneme that either matched or mismatched the phoneme they were instructed to produce in their minds. The results showed that production of the silent phoneme resulted in N1 suppression, but only if the silent phoneme matched that of the phoneme the participant heard, demonstrating that the sensory attenuation phenomenon could be extrapolated to inner speech as well.

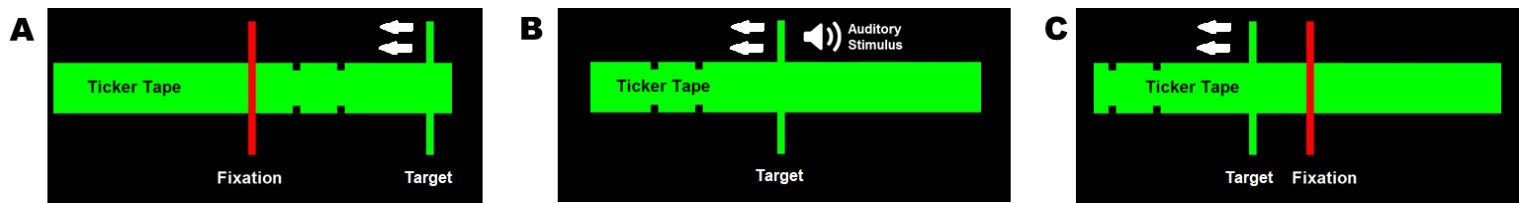


Figure 1. 5. A schematic of the tickertape feature of the experimental paradigm.

Participants observe the red fixation line while the green target line moves towards the fixation line (Panel A). Sound onset occurs when the two lines intersect (Panel B). One of the main advantages of using this design is that because all conditions use the same visual animation, temporal predictability can be controlled across conditions. Adapted from Whitford et al. (2017) and Jack et al. (2019).

In the context of the present thesis, the key advantage of the experimental paradigm described above is that by using the ticker tape design, one can control for temporal predictability across conditions as sounds are temporally predictable in the *auditory* condition. Furthermore, as will be discussed in more detail in the subsequent empirical chapters, using a modified version of this paradigm allows us to isolate the effect of *sense of agency* (Experiments 1 and 2, which together constitute Chapter 2) and *action-effect contingency* (Experiments 3 and 4, which together constitute Chapter 3) on the sensory attenuation effect. The purpose of Experiment 5 (which constitutes Chapter 4) was to also to investigate *action-outcome contingency* on the sensory attenuation effect but was conducted using a more traditional self-stimulation paradigm to build upon the results observed in Chapter 3 and relate these to the existing literature.

Chapter 2: Sensory attenuation in the absence of movement

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2. 1. Preamble

As outlined in Chapter 1, most studies investigating the phenomenon of sensory attenuation have used an experimental paradigm that links motor actions to resulting sounds. In these studies, participants generally press a button that immediately results in a sound (the *active* condition) or passively listen to a physically identical sound (the *passive* condition). These studies have generally found evidence of N1 suppression wherein sounds in the *active* condition elicit N1 components with smaller amplitudes than sounds in the *passive* condition, despite the sounds themselves being physically identical. However, the majority of these previous studies have been unable to control for potential confounds relating to the temporal predictability of the sounds, the presence of motor-evoked potentials, and between-condition differences in sense of agency over the sound. With relation to the first, sounds in the *active* condition are more temporally predictable than sounds in the *passive* condition, because sounds in the *active* condition are being generated by participants at a time of their choosing, whereas sounds in the *passive* condition are not. This between-condition difference in temporal predictability is a potential confound which may influence the results. Secondly, sounds in the *active* condition are caused via willed motor actions. These motor actions generate motor-evoked potentials which potentially contribute to the obtained ERPs, leading to systematic differences between the ERPs generated in the *active* and *passive* conditions.

Finally, although not a direct issue stemming from the experimental paradigm, there is also the issue that motor actions are tied to sounds in the *active* condition, meaning that participants' sense of agency over the sound is different between the *active* and *passive* conditions.

The experiments described in the present chapter aim to address the potential confounds listed above by disentangling the motor action from the resulting sound. In this chapter, sounds are triggered via either willed inactions (Experiment 1) or by willed actions that are temporally divorced from the sound (Experiment 2). Sounds are made equally predictable across both the *active* and *passive* conditions because sound onset is locked to markers on an external cue (a moving tickertape) as opposed to the participant's actions *per se*. Because sounds are also divorced from motor actions, motor-evoked potentials do not contribute to the ERPs obtained from either the *active* or *passive* conditions. These changes also allow for the investigation of the effect of between-condition differences in *sense of agency* over the sound, as a participant's control over the sound onset is not tied to the presence of a coincident motor action. This novel design allows to explore the phenomenon of sensory attenuation and its neurophysiological correlates while minimising the potential for between condition differences in temporal predictability, motor-evoked activity and sense of agency over the sounds.

2.2. Abstract

Sensory attenuation is the phenomenon that stimuli generated by willed motor actions elicit a smaller neurophysiological response than those generated by external sources. It has mostly been investigated in the auditory domain, by comparing ERPs evoked by self-initiated (*active* condition) and externally generated (*passive* condition) sounds. The mechanistic basis of sensory attenuation has been argued to involve a duplicate of the motor command being used to predict sensory consequences of self-generated movements. An alternative possibility is

that the effect is driven by between-condition differences in participants' sense of agency over the sound. In this paper, we disambiguated the effects of motor-action and sense of agency on sensory attenuation with a novel experimental paradigm. In Experiment 1, participants watched a moving, marked tickertape while EEG was recorded. In the *active* condition, participants chose whether to press a button by a certain mark on the tickertape. If a button-press had not occurred by the mark, then a tone would be played one second later. If the button was pressed prior to the mark, the tone was not played. In the *passive* condition, participants passively watched the animation, and were informed about whether a tone would be played on each trial. The design for Experiment 2 was identical, except that the contingencies were reversed (i.e., a button-press by the mark led to a tone). The results were consistent across the two experiments: while there were no differences in N1 amplitude between the *active* and *passive* conditions, the amplitude of the Tb component was suppressed in the *active* condition. The amplitude of the P2 component was enhanced in the *active* condition in both Experiments 1 and 2. These results suggest that motor-actions and sense of agency have differential effects on sensory attenuation to sounds and are indexed with different ERP components.

2. 3. Introduction

Sensory attenuation is the phenomenon that self-generated sensations feel less salient, and evoke a smaller neurophysiological response, than externally generated sensations, even when the evoking stimuli are physically identical (Hughes, Desantis, & Waszak, 2013). The neurophysiological aspect of sensory attenuation has been most commonly investigated in the auditory domain, by using EEG/MEG to compare the evoked response to self-initiated and externally initiated sounds (Schafer & Marcus, 1973; Horváth, 2015). There is substantial evidence that certain components of the auditory-evoked potential are reduced in amplitude when participants listen to sounds initiated by their own motor actions, compared to when they passively listen to the same sound. This effect has been most consistently observed with the N1 component (Bäß, Jacobsen, & Schröger, 2008; Elijah, Pelley, & Whitford, 2018; Mifsud et al., 2016; Neszmeélyi & Horváth, 2017; Oestreich et al., 2016; van Elk et al., 2014; Pinheiro et al., 2019), but has also been identified with the Tb (SanMiguel, Todd, & Schröger, 2013; Saupe et al., 2013) and P2 components (Knolle et al., 2012; Horváth & Burgyán, 2013).

The N1 component of the auditory-evoked potential is a negative deflection that generally appears about 50-150 ms after audio stimulus onset (Näätänen & Picton, 1987), and is believed to be generated in the auditory cortices (Näätänen & Picton, 1987). The N1 is not a unitary component; in contrast, there are believed to be at least three obligatory sources for the N1, with Components 1 and 2 reflecting sound processing in the primary and secondary auditory. The amplitude of the N1 component has been shown to index the physical features of sounds, most notably auditory intensity; that is, loud sounds tend to elicit larger N1 amplitudes than soft sounds (Beagley & Knight, 1967; Picton, Goodman, & Bryce, 1970; Adler & Adler, 1989).

The Tb is a negative-going component that occurs about 130 – 170 ms after sound onset and is believed to be generated within the secondary auditory cortex (Wolpaw & Penry, 1975; Gallinat et al., 2002; Tonnquist-Uhlen et al., 2003; Rihs et al., 2013), potentially in the vicinity of Wernicke's area (Alain, Woods, & Covarrubias, 1997). While the functional significance of the Tb component has not been definitively established, it has been implicated in auditory processing, particularly of 'high level' auditory stimuli including music and language (Giard et al., 1994; Tonnquist-Uhlen et al., 2003; Shahin, Bosnyak, Trainor, & Roberts, 2003; Langers, Backes, & van Dijk, 2007; Harpaz, Levkovitz & Lavidor, 2009; Hämäläinen et al., 2011; Bruneau et al., 2003; Azouz et al., 2014).

The P2 is a positive-going component occurs about 150 – 250 ms after sound onset. Several sources are thought to underlie the P2, with one in the PT (planum temporale) and Brodmann Area 22 (the auditory association complex) (Crowley & Colrain, 2004). Although its functional significance is not clear, the P2 component has been associated with attention and categorization processes (García-Larrea, Lukaszewicz, & Mauguière, 1992; Crowley & Colrain, 2004, Lijffijt et al., 2009). Further evidence has also linked the P2 component to working memory processes (Lefebvre et al., 2005; Finnigan et al., 2011; Duzcu et al., 2019).

The mechanistic basis of sensory attenuation has been argued to involve an internal forward model in which the brain uses a copy of the outgoing motor command ('efference copy') to make predictions ('corollary discharges') about the expected sensory consequences of self-initiated movements (Miall & Wolpert, 1996). Sensory attenuation has been conceptualized as a specific example of predictive coding, in which sensory predictions and sensory feedback are compared, and observed deviations (i.e., prediction errors) are used to update and improve the sensory predictions (Crapse & Sommer, 2008; Poulet & Hedwig, 2007; Schütz-Bosbach & Prinz, 2007; Subramanian, Alers, & Sommer, 2019; Straka, Simmers, & Chagnaud, 2018).

Sensory attenuation has often been assumed to result from the comparison between sensory predictions and sensory feedback in the internal forward model. This implies that sensory attenuation is dependent on the presence of the motor action by which the sensory predictions are generated (Bäß et al., 2008; Hughes et al., 2013). However, an alternative possibility is that the effect is driven by participants' sense of agency in the self-initiation condition. Sense of agency refers to “*the feeling of control over actions and their [sensory] consequences*” (Moore, 2016). In a typical self-stimulation paradigm, the *active* condition consists of the participant repeatedly performing a motor action (e.g., a button-press) to elicit a sequence of sounds. In the *passive* condition, the same sequence of sounds is presented without the participant having to perform any motor action. A consequence of this design is the participant has control over the sounds in the *active* condition but not the *passive* condition. This raises an important question: to what extent is the sensory attenuation effect driven by the between-condition differences in sense of agency as opposed to the presence of the motor action *per se*? Rather than merely being a byproduct of comparator processes, as has been suggested (Synofzik, Vosgerau, & Newen, 2008), sense of agency may instead have a pivotal causal role in sensory attenuation.

Most previous studies of sensory attenuation have conflated participants' sense of agency with the motor action as the two co-occur in a typical self-stimulation paradigm. We attempted to dissociate these two factors by means of a novel experimental paradigm. In our paradigm, participants had to decide, on every trial, as to whether or not to press a button. This decision determined whether a sound would subsequently be presented after a significant delay. In Experiment 1, sounds were only played on trials in which participants did *not* press the button. In other words, participants had control over whether and when they heard the sounds, but their sense of agency did not result from a motor action. Sounds in

these *active* blocks were compared to sounds presented in *passive* blocks, where participants did not perform actions on any trials. If the N1, Tb and/or P2 components are associated with a participant's sense of agency over the sounds – independent of the presence of a motor action – then this would manifest as differences in component amplitude between the *active* and *passive* blocks.

2. 4. Method

2. 4. 1. Experiment 1

2. 4. 1. 1. Participants

Forty-four undergraduate students from the University of New South Wales (Sydney, Australia) participated in the study in exchange for course credit. All participants gave written informed consent prior to the experiment. Two participants were removed from analysis due to insufficient number of artifact-free epochs (as described in EEG Recording and Analysis) leaving a final sample of $N = 42$ participants (mean age = 22 years, $SD = 4.3$, 21 females). Given our sample size of $N = 42$, this study could detect an effect size of $\eta_p^2 = 0.15$ at power = 80% with alpha = 0.05. The power analysis was conducted using G*Power software (version 3.1.9.6; Faul et al., 2007). The study was approved by the Human Research Ethics Advisory Panel (Psychology) at the University of New South Wales.

2. 4. 1. 2 Stimuli, Materials, and Procedure

The audio stimulus was a sinusoid tone of frequency 1000 Hz (100 ms duration, with a 5 ms rise/fall time). Audio stimuli were sent to participants through Sennheiser HD 210 headphones. Audio input/output was controlled by a specially written MATLAB script using the Psychophysics Toolbox (Brainard, 1997). Participants made responses by pressing the space bar of a low-latency keyboard (DuckyShine 4, 1000 Hz report rate). Visual stimuli were displayed on a high-performance monitor (24-inch, BenQ XL2420T).

During each trial, participants observed a visual animation, which was adapted from the paradigm employed by Whitford et al. (2017) and Jack et al. (2019). The animation lasted for about 6 seconds. A schematic of the animation is presented in Figure 1. The animation consisted of a central red fixation line that sat in the middle of a green horizontal bar, which we refer to as the ‘ticker tape’. Participants were instructed to keep their eyes fixated on the fixation line during the trial. There was also a blue ‘decision line’ and a green ‘trigger line’ located on the right side of the ticker tape. The trigger line was initially positioned on the far-right hand side of the ticker tape; the decision line was positioned to the left of the trigger line (Figure 1A).

Upon commencement of the trial, after a 1 s delay, both the decision line and the trigger line started to move towards the fixation line at a constant rate of 6.5 degrees per second. Approximately 3 s after the lines started moving, the decision line intersected the fixation line. The trigger line intersected the fixation line one second later, i.e., approximately 4 s after the lines initially started moving. The auditory stimulus was presented when the trigger line intersected with the fixation line (see Figure 1). The lines continued to move for another 1 s, before the animation concluded, and the trial was completed.

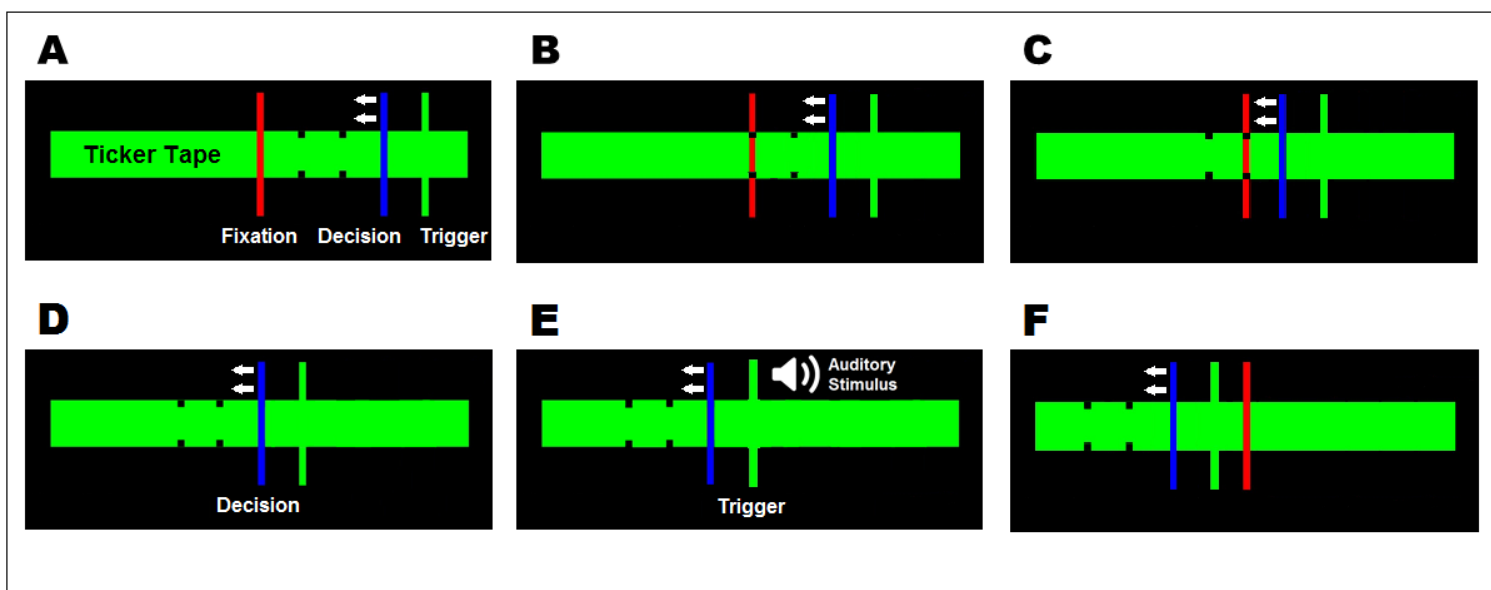


Figure 2. 1. A schematic of the experimental protocol. In the *active* condition, participants were instructed to fixate their eyes on the central red fixation line (Panel A). After a one second delay, the blue decision line and the green trigger line moved slowly towards the central red fixation line at a rate of 6.5 degrees per second (Panel B-C). On each trial, participants were told that they had to decide whether or not to press the space bar on the keyboard by the decision time (i.e., the time at which the decision line intersected the fixation line) (Panel D). In Experiment 1, participants were told that if they did not press the space bar by the decision time, this would cause the audio stimulus to be played at trigger time (i.e., the time at which the trigger line intersected the fixation line) (Panel E). Conversely, participants were told that if they did press the space bar by decision time, the audio stimulus would not play at the trigger time. In Experiment 2, this contingency was reversed. That is, if the participant did not press the space bar before the decision time, the audio stimulus was not played at the trigger time; conversely, if the participant did press the space bar before the decision time, this caused the audio stimulus to be played at the trigger time. In the *passive* condition of both experiments, participants observed the same animation but did not perform any motor actions. The audio stimulus was played on exactly half of the trials in the *passive* condition. Participants were informed at the start of each trial whether or not the audio stimulus would be played. *Passive* conditions were identical across both experiments.

There were two conditions in the experiment: the *active* condition and the *passive* condition. In the *active* condition, participants had the option of pressing the space bar on the keyboard at any time up until the point at which the decision line intersected the fixation line (hereon referred to as the ‘decision time’). Participants were told that if they *did not* press the button by the decision time (Figure 1D), this would cause the audio stimulus to be played at the point at which the trigger line intersected the fixation line (hereon referred to as the ‘trigger time’) (Figure 1E). In contrast, the participant was told that if they *did* press the button before the decision time, the audio stimulus would not be played. In other words, the participant had complete control over whether they heard the audio stimulus on any given trial. Participants were asked to press the button on approximately half the trials, and to avoid conforming to any obvious pattern of responses. At the start of every trial, participants were reminded (by means of instructions on the screen) as to what their options were and what the consequences of those options were.

In the *passive* condition, participants watched the same animation as in the *active* condition but were not required to perform any action. The auditory stimulus was presented on 50% of trials (randomly selected) at the trigger time. At the start of every trial, participants were informed (by means of instructions on the screen) as to whether the audio stimulus would be played on that trial.

The experiment consisted of four *active* blocks and *four passive* blocks¹, totaling eight blocks for the whole experiment. Each block consisted of 30 trials. The order of the blocks alternated between *active* and *passive* blocks, and the starting block was counterbalanced between participants.

2. 4. 1. 3. EEG Recording and Analysis

EEG was recorded with a BioSemi ActiveTwo system from 64 Ag/EgCl active electrodes (P1, FPz, FP2, AF7, AF3, AFz, AF4, AF8, F7, F5, F3, F1, Fz, F2, F4, F6, F8, FT7, FC5, FC3, FC1, FCz, FC2, FC4, FC6, FT8, T7, C5, C3, C1, Cz, C2, C4, C6, T8, TP7, CP5, CP3, CP1, CPz, CP2, CP4, CP6, TP8, P9, P7, P5, P3, P1, Pz, P2, P4, P6, P8, P10, PO7, PO3, POz, PO4, PO8, O1, Oz, O2, Iz). In the BioSemi ActiveTwo system, the ‘ground’ electrode is replaced with two separate electrodes – an ‘active’ CMS (Common Mode Sense) electrode, and a ‘passive’ DRL (Driven Right Leg) electrode. These electrodes are arranged in a feedback loop which drives the average potential of the participant (i.e., the Common Mode

¹ Although the conditions in current study are called the *active* and *passive* conditions, they differ significantly from those of a typical self-stimulation paradigm. In a typical self-stimulation paradigm (Schafer & Marcus, 1973), the *active* condition consists of a participant repeatedly performing a motor action (e.g., a button-press) in order to elicit a sequence of tones. In the *passive* condition, the same sequence of tones is presented without the participant having to perform any action. In the typical self-stimulation paradigm, tones immediately followed the button-press in the *active* condition. The *active* and *passive* conditions of the current study differ in that tones are not time-locked to a participant’s decision to elicit the tone. Additionally, tones in the *active* and *passive* conditions were both triggered at exactly the same point of the animation (i.e., at the ‘trigger time’). We retained the *active* and *passive* condition names given that the *active* condition of both the traditional and current experiments require participants’ control while sounds in both *passive* conditions are out of the control of participants.

voltage) as close as possible to the reference voltage (i.e., the ‘zero’) of the amplifier. See www.biosemi.com for more details. A vertical electrooculogram (EOG) was recorded by placing an electrode above and below the left eye; a horizontal EOG was recorded by placing an electrode on the outer canthus of each eye. Electrodes were also placed on each mastoid, and the nose. During data acquisition, the reference was composed of sites CMS and DRL, and the sampling rate was 2,048 Hz.

For data analyses, we re-referenced the EEG data offline to the nose electrode, as is common in studies investigating the components-of-interest, and necessary for extracting the Tb component (Näätänen & Picton, 1987; Woods, 1995; SanMiguel et al., 2013). Data were band-pass filtered from 0.1 to 30Hz using a half-amplitude phase-shift-free Butterworth filter, then notch filtered (50Hz) to remove mains artefact. The filtered data were segmented into 500 ms epochs, from -100 ms pre-stimulus to 400 ms post-stimulus. Only trials in which the auditory stimulus were played were analyzed. Epochs were baseline-corrected to the mean voltage from -100 to 0 ms. We corrected the epochs for eye blinks and movement artefacts using the technique described in Gratton, Coles, and Donchin (1983) and Miller, Gratton, and Yee (1988). We excluded all epochs with signals exceeding peak-to-peak amplitudes of 200 μ V and had a maximal allowed voltage step of 50 μ V/ms. We analysed the amplitude of the N1, Tb and P2 components of the auditory-evoked potential. Component amplitude was calculated as the average voltage within 30 ms time-window, the center of which was defined using the collapsed localiser approach (Luck & Gaspelin, 2017). The collapsed localiser approach is a technique whereby one first averages (or ‘collapses’) the ERP waveforms across all conditions for all participants. The components-of-interest (e.g., N1, Tb, P2) are identified on this ‘collapsed’ waveform, and a time-window is centred around these peaks, which is then used for the statistical analysis of the original (or ‘uncollapsed’) waveforms (Luck & Gaspelin, 2017).

For the N1 and P2 components, mean voltage in the analysis window was submitted to a 2 (Condition: *active*, *passive*) x 9 (Electrode) repeated-measures ANOVA. Electrodes of interest for the N1 component were the Fz, F1, F2, FCz, FC1, FC2, Cz, C1, and C2 electrodes. The electrodes of interest for the P2 component were the FCz, FC1, FC2, Cz, C1, C2, CPz, CP1, and CP2 electrodes. Electrode selection for the N1 and P2 components were based on recommendations by the manuscript reviewer at time of publishing. The mean voltage of the Tb component in the analysis window was submitted to a 2 (Condition: *active*, *passive*) x 2 (Electrode: T7, T8) repeated-measures ANOVA. Electrodes for the Tb component (T7 and T8) were based on recommendations by Tonnquist-Uhlen et al. (2013) and SanMiguel et al. (2013).

2. 4. 1. 4. Experiment 1 Results

There was an average of 55.9 (SD = 11.6) usable epochs in the *active* condition and 53.6 (SD = 9.8) in the *passive* condition. If a participant pressed the button on exactly half the trials in the *active* condition, and if all epochs were artefact-free, there would be 60 usable epochs in the *active* condition. Similarly, if participants followed instructions perfectly, and if all epochs were artefact-free, there would be 60 usable epochs in the *passive* condition. The number of sound trials were obtained and compared across the *active* and *passive* conditions. There were 62.29 sound trials (SD = 5.85) in the *active* condition and 59.31 sound trials (SD = 2.45) in the *passive* condition. The chi-square test yielded $\chi^2(41, N = 42) = 22.55, p = .991$.

N1

Figure 2A shows the N1 component analysis elicited in the *active* and *passive* conditions. N1 was maximal at electrode FCz for both conditions and showed the expected fronto-central topography. The time-window for the N1 analysis was centered at 89.8 ms and extended from 74.8 – 104.8 ms. The main effect of Condition was not statistically significant, $F(1, 41) = .47$,

$p = .497$, $\eta_p^2 = 0.01$. Similarly, the *Condition*×*Electrode* interaction was not statistically significant, $F(1, 41) = 1.26$, $p = .266$, $\eta_p^2 = 0.03$. The results indicate that N1 amplitude was not significantly different between the active and passive conditions.

Tb

Figure 2B show the Tb component analysis elicited in the *active* and *passive* conditions. Tb was maximal at electrodes T7 and T8 for both conditions and showed the expected temporal-lobe topography. The time-window for the Tb analysis was centered at 124.5 ms and extended from 109.5 – 139.5 ms. The repeated measures ANOVA yielded a significant main effect of *Condition*, $F(1, 41) = 4.74$, $p = .035$, $\eta_p^2 = 0.10$. The *Condition*×*Electrode* interaction was not significant, $F(1, 41) = 1.39$, $p = .246$, $\eta_p^2 = 0.03$. The results suggest that the Tb amplitude of the *active* condition was suppressed relative to the amplitude in the *passive* condition, and the effect was not driven by any one electrode.

P2

Figure 2C shows the P2 component analysis elicited in the *active* and *passive* conditions. P2 was maximal at electrode Cz for both conditions and showed the expected central topography. The time-window for the P2 analysis was centered at 182.6 ms and extended from 167.6 – 197.6 ms. The main effect of *Condition* was significant, $F(1, 41) = 10.30$, $p = .003$, $\eta_p^2 = 0.20$. The *Condition*×*Electrode* interaction was not significant, $F(1, 41) = .42$, $p = .907$, $\eta_p^2 = 0.01$. The results suggest that the P2 amplitude of the active condition was enhanced relative to the amplitude in the passive condition, and the effect was not driven by any individual electrode.

2. 4. 1. 5. Experiment 1 Discussion

In Experiment 1, participants were able to determine whether a sound was presented by means of a prior-made decision; specifically, if participants chose *not* to press the button

by the decision time, this resulted in the sound being presented at the trigger time. The upshot of this was that participants had complete control over the sound delivery, but this control was not a consequence of a motor action. The results revealed that while the amplitude of the N1 component did not differ between the *active* and *passive* conditions, the amplitudes of the Tb and P2 components did, with Tb suppressed in the *active* condition, and P2 enhanced in the *active* condition.

The aim of Experiment 2 was to determine whether the observed results were dependent on the participant's decision to hear the sound being indexed by a non-action (i.e., in which participants implemented their decision to hear a subsequent tone by choosing *not* performing a motor action), or whether the same results would be observed when the participants decision was indexed by a motor-action that was temporally distant (i.e., occurred well prior) to the sound.

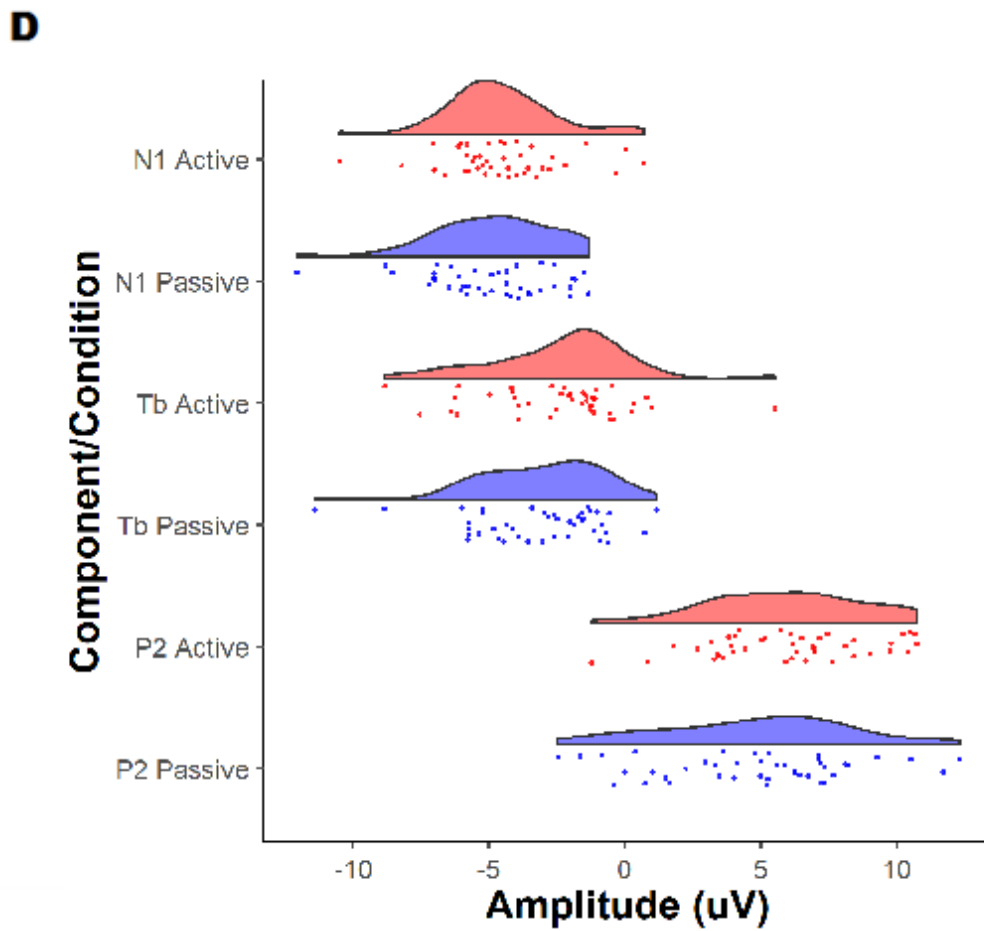
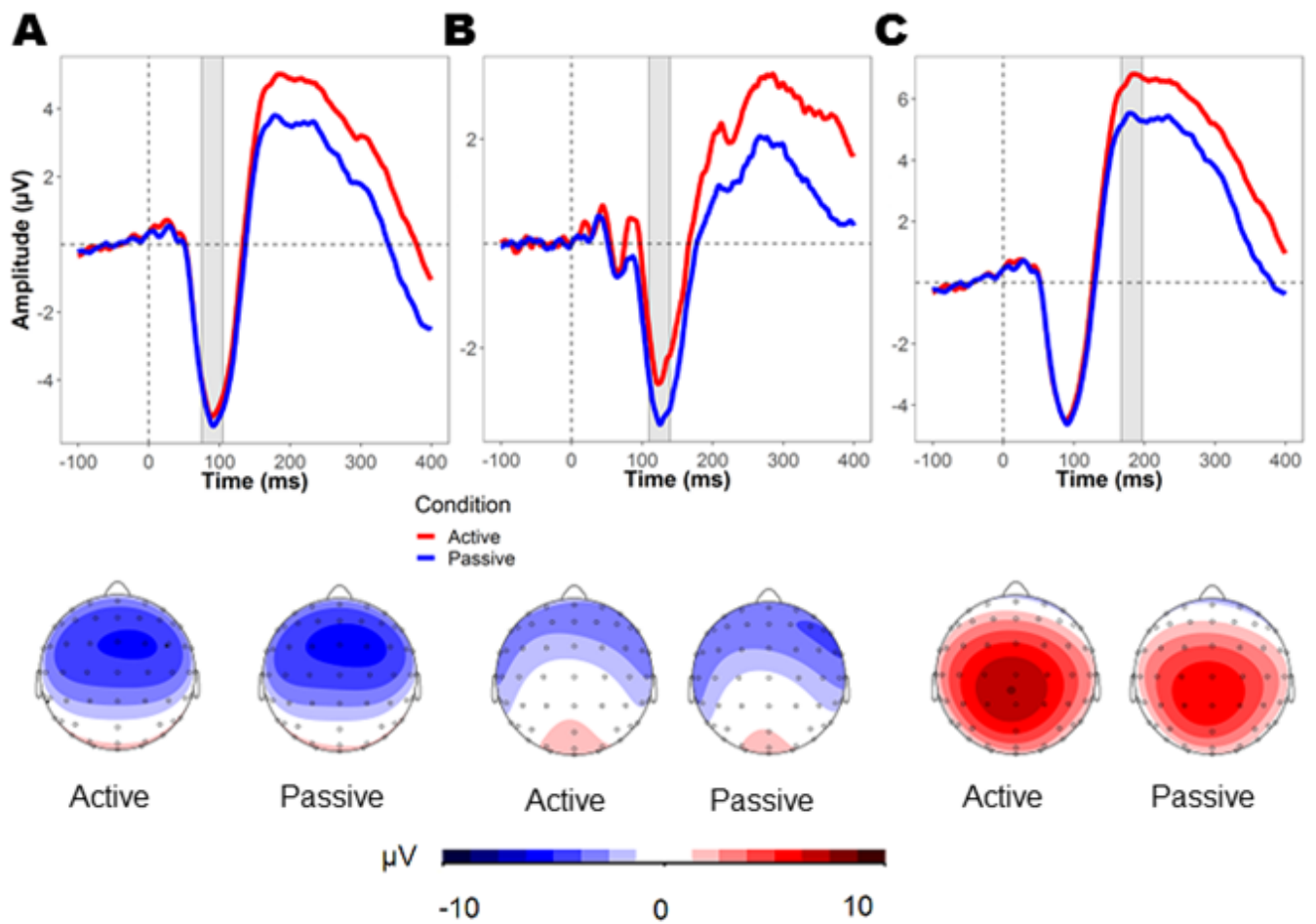


Figure 2. 2. Experiment 1: Waveforms showing ERPs elicited by the *active* condition and the *passive* condition in addition to corresponding topographic mappings. (A) N1 component (Fz, F1, F2, FCz, FC1, FC2, Cz, C1, C2): 74.8 – 104.8 ms. (B) Tb component (T7, T8): 109.5 – 139.5 ms. (C) P2 component (FCz, FC1, FC2, Cz, C1, C2, CPz, CP1, CP2): 167.6- 197.6 ms. (D) Raincloud graph (Allen et al., 2019) containing density plots and scatter plots of mean amplitudes for the N1, Tb, and P2 components for the *active* and *passive* conditions.

2. 4. 2. Experiment 2

2. 4. 2. 1. Participants

Forty-seven undergraduate students from the University of New South Wales (Sydney, Australia) participated in the study in exchange for course credit ($N = 47$). All participants gave written informed consent prior to the experiment. Participants' mean age was 20.3 years ($SD = 5.6$), and 29 of the participants were female. Given our sample size of $n = 47$, this study could detect an effect size of $\eta_p^2 = 0.18$ at power = 80% with $\alpha = 0.05$. The power analysis was conducted using G*Power software (version 3.1.9.6; Faul et al., 2007). The study was approved by the Human Research Ethics Advisory Panel (Psychology) at the University of New South Wales.

2. 4. 2. 2. Stimuli, Materials, and Procedure

The stimuli and materials were identical to Experiment 1. The only difference between the experiments was the action-effect contingency in the *active* condition. In Experiment 1, the audio stimulus was played if the participant elected not to press the button before the decision time. In Experiment 2, this contingency was reversed: the audio stimulus was played *only* if the participant pressed the button prior to the decision time. As in Experiment 1, the audio stimulus was played at the trigger time, which occurred 1 s after the decision-time which, to reiterate, was the last possible time the participant could elect to press the button; trials in which the participant pressed the button after the decision-time were excluded.

2. 4. 2. 3. EEG Recording and Analysis

The EEG recording and analysis were identical to Experiment 1.

2. 4. 2. 4. Experiment 2 Results

There was an average of 60.3 (SD = 7.2) usable epochs in the *active* condition and 57 (SD = 1.9) in the *passive* condition. The number of sound trials were obtained and compared across the *active* and *passive* conditions. There were 61.85 sound trials (SD = 6.31) in the *active* condition compared to 59.06 sound trials in the *passive* condition (SD = 1.13). The chi-square test yielded $X^2(46, N = 47) = 29.62, p = .971$.

N1

Figure 3A shows the N1 component analysis elicited in the *active* and *passive* conditions. N1 was maximal at electrode FCz for both conditions and showed the expected fronto-central topography. The time-window for the N1 analysis was centered at 84 ms and extended from 69 – 99 ms. The main effect of Condition was not statistically significant, $F(1, 46) = 1.18, p = .283, \eta_p^2 = 0.03$. The *ConditionxElectrode* interaction was also not statistically significant, $F(1, 46) = 1.26, p = .266, \eta_p^2 = 0.03$.

Tb

Figure 3B show the Tb component analysis elicited in the *active* and *passive* conditions. Tb was maximal at electrodes T7 and T8 for both conditions and showed the expected temporal topography. The time-window for the Tb analysis was centered at 120.6 ms and extended from 105.6 – 135.6 ms. The repeated measures ANOVA yielded a significant main effect of *Condition*, $F(1, 46) = 11.12, p = .002, \eta_p^2 = 0.20$, as well as a significant *ConditionxElectrode* interaction, $F(1, 46) = 9.08, p = .004, \eta_p^2 = 0.20$. The results suggest that the Tb amplitude of

the *active* condition was suppressed relative to the amplitude in the *passive* condition, and the effect was driven by the T7 electrode, $t(46) = 3.982, p < .001, d = 0.58$.

P2

Figure 3C shows the P2 component analysis elicited in the *active* and *passive* conditions. N1 was maximal at electrode Cz for both conditions and showed the expected central topography. The time-window for the P2 analysis was centered at 181.2 ms and extended from 166.2 – 196.2 ms. The repeated measures ANOVA yielded a significant main effect of Condition, $F(1, 46) = 7.21, p = .010, \eta_p^2 = 0.14$, as well as a significant *ConditionxElectrode* interaction, $F(1, 46) = 3.16, p = .002, \eta_p^2 = 0.06$. The results of this additional analysis suggest that the P2 in the *active* condition was enhanced relative to the *passive* condition, with the effect being driven by lateral electrodes. Subsequent paired-sample t-tests showed that the electrodes of significance were the FC1 ($t(46) = 3.805, p < .001, d = 0.56$), FC2 ($t(46) = 3.646, p < .001, d = 0.53$), C1 ($t(46) = 3.682, p < .001, d = 0.54$), C2 ($t(46) = 3.119, p = .003, d = 0.46$), CP1 ($t(46) = 3.222, p = .002, d = 0.47$), and CP2 ($t(46) = 2.278, p = .027, d = 0.33$) electrodes. As the *ConditionxElectrode* interaction and the subsequent simple tests were exploratory analyses, no correction for multiple comparisons were performed.

See Figure 4 for a summary of results for both experiments.

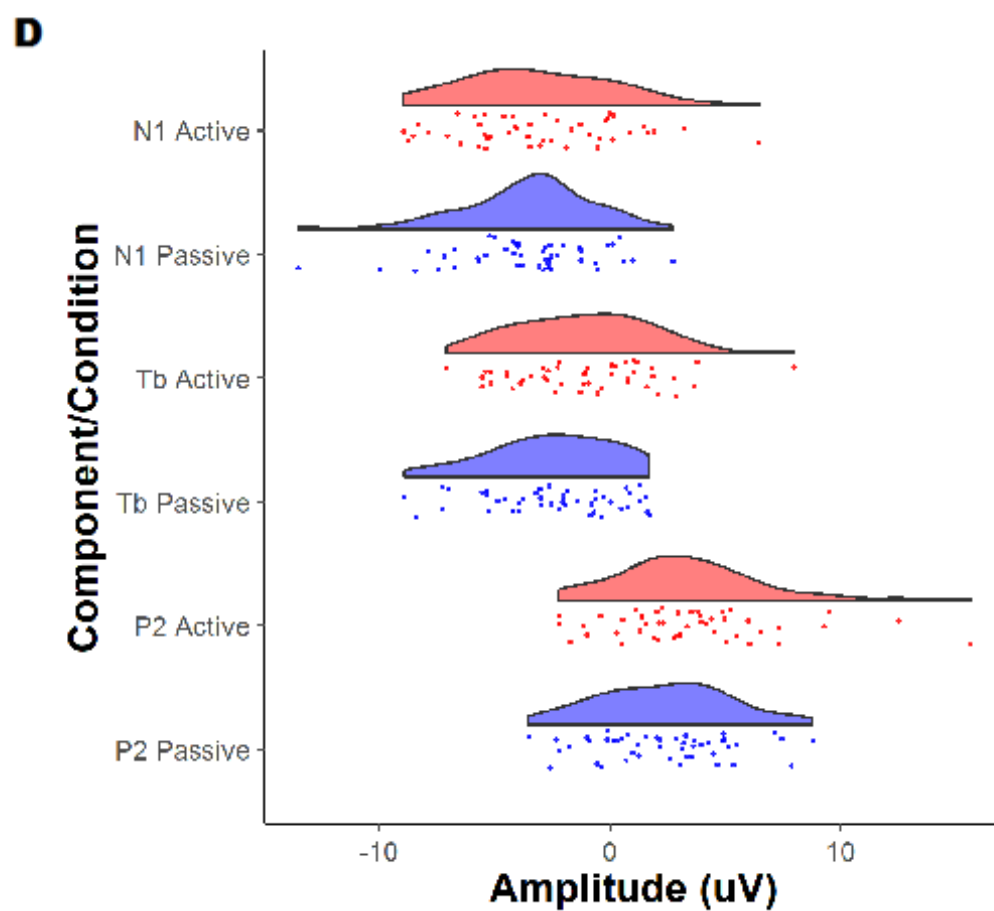
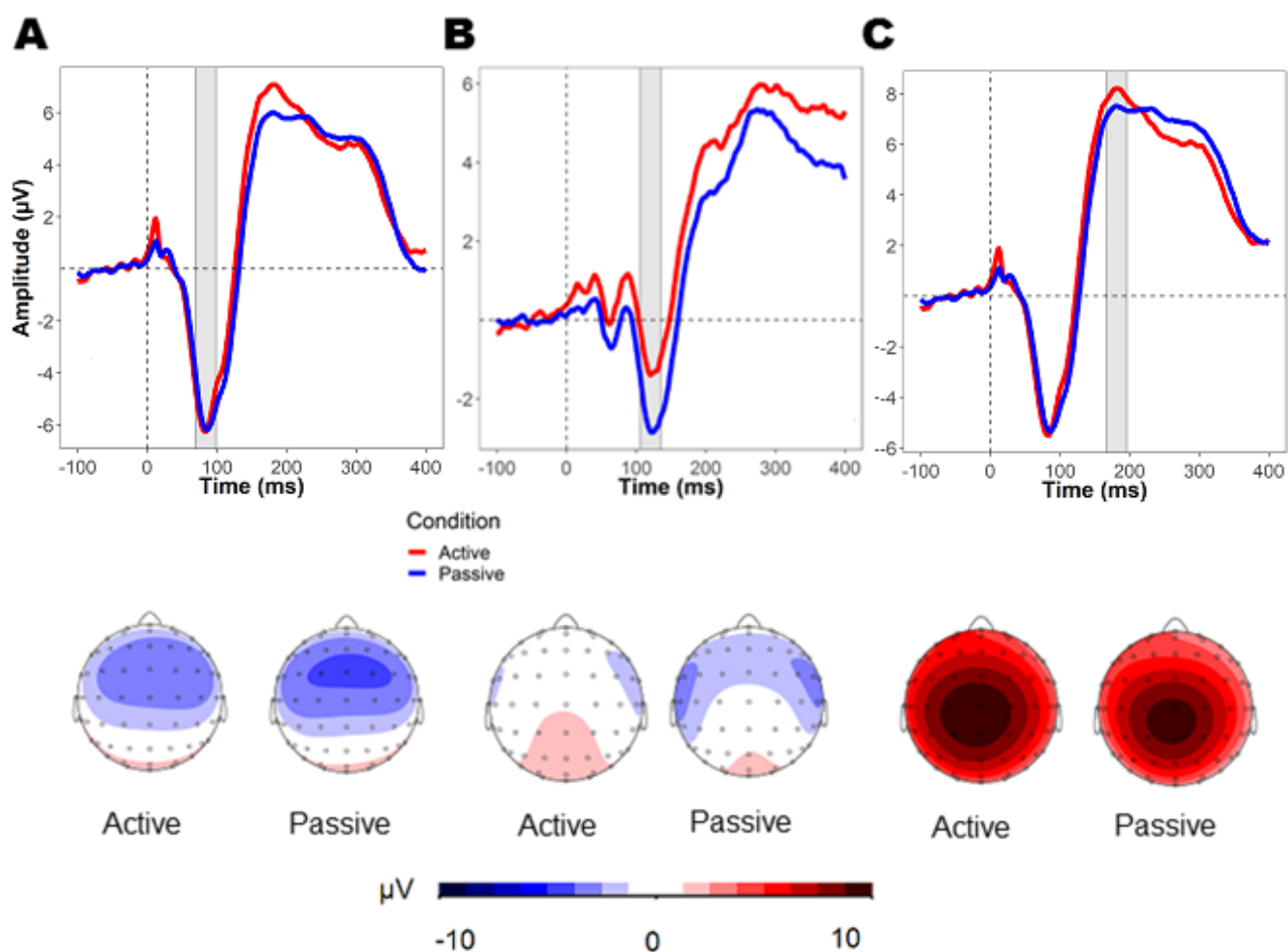


Figure 2. 3. Experiment 2: Waveforms showing ERPs elicited by the *active* condition and the *passive* condition in addition to corresponding topographic mappings. (A) N1 component (Fz, F1, F2, FCz, FC1, FC2, Cz, C1, C2): 69 – 99 ms. (B) Tb component (T7, T8): 105.6 – 135.6 ms. (C) P2 component (FCz, FC1, FC2, Cz, C1, C2, CPz, CP1, CP2): 166.2- 199.2 ms. (D) Raincloud graph (Allen et al., 2019) containing density plots and scatter plots of mean amplitudes for the N1, Tb, and P2 components for the *active* and *passive* conditions.

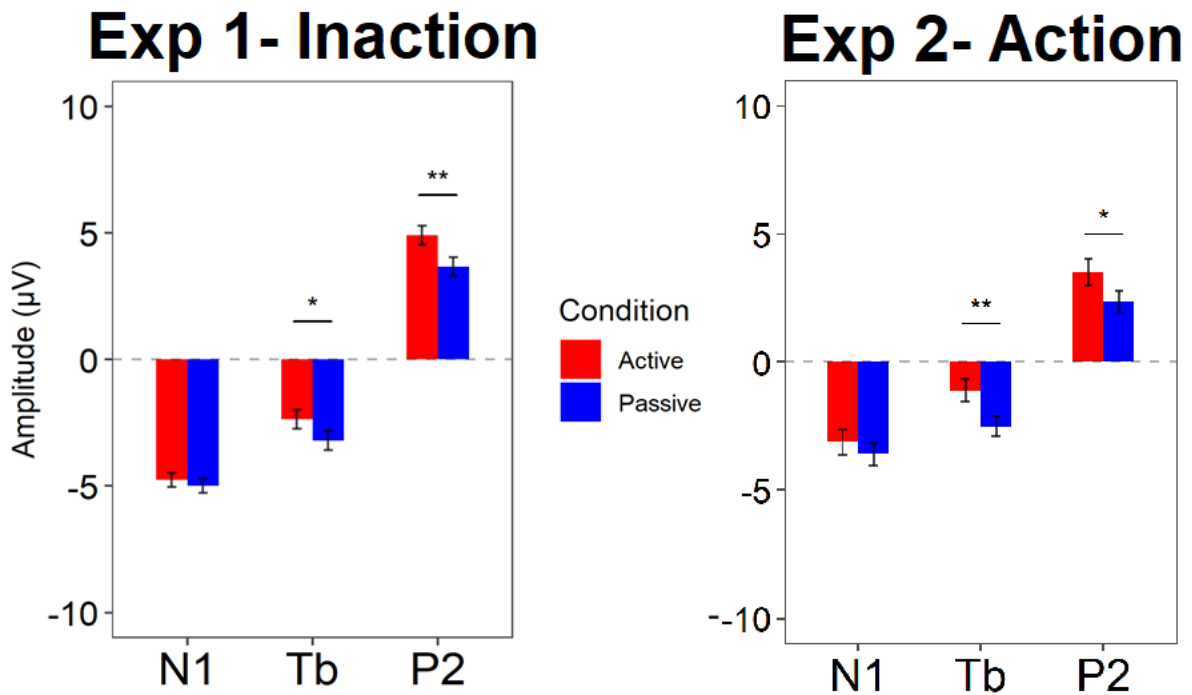


Figure 2. 4. Bar graphs of Experiments 1 and 2 illustrating mean amplitudes for the N1, Tb, and P2 components for the *active* and *passive* condition. Error bars show the standard error of paired differences (SEPD; Pfister & Janczyk, 2013). Asterisks represent levels of significance (* $p < .05$; ** $p < .01$).

2. 5. General Discussion

In this study, we set out to investigate whether sensory attenuation (operationalized as suppression of the N1, Tb, and P2 components of the auditory-evoked potential) occurs when a participant has complete control over the occurrence of a sound – and thus a sense of agency over the sound – but does not perform a motor action (Experiment 1) or performs a motor action that is temporally distant to the sound (Experiment 2). The results were similar across experiments. In both experiments, the Tb component, but not the N1 component, was

attenuated in the *active* condition relative to the *passive* condition. The P2 component was enhanced in the *active* condition relative to the *passive* condition for both Experiments 1 and 2. As summarized in Figure 4, the results of these two experiments suggest that the effect of motor-based predictions on sensory attenuation can be dissociated from those associated with one's sense of agency *per se*, as they seemingly impact on different components of the auditory-evoked potential. Although we have used the label "sense of agency", we acknowledge that it is not possible to differentiate the effect of participants' 'sense of agency' from their 'agency *per se*' in the current experiment.

Our experimental design did not require us to control for motor-related differences in the *active* condition relative to the *passive* condition. Many iterations of the self-stimulation paradigm include a third *motor* condition wherein participants press a button that does not result in a sound. The ERP of this 'motor-only' condition is subtracted from the ERP of the *active* condition, resulting in an audio-only ERP that is ostensibly motor-controlled. However, several arguments have been made that query the assumptions behind this subtraction (Neszmélyi & Horváth, 2017; Neszmélyi & Horváth, 2019; Horváth, Bíró, & Neszmélyi, 2018). In Experiment 1 of the current study, it was a willed *inaction* that resulted in sounds. In Experiment 2, the time between the action and the sound was at least 1 second, and varied substantially between trials and participants, as the action was not time-locked to the sound. Our design also attempted to control for between-condition differences in temporal predictability and temporal control (see Lange, 2011; Hughes et al., 2013); the temporal onset of the tone was equally predictable and uncontrollable in both the *active* and *passive* conditions, as the tone only ever occurred at the time at which the trigger line and fixation line intersected.

In both experiments, we found no difference in N1 amplitude between the *active* and *passive* conditions. This stands in contrast to most previous self-stimulation studies that have

observed smaller N1 amplitudes in the *active* condition relative to the *passive* condition (i.e., N1-suppression) (Baess et al., 2011; Bäß, Jacobsen, & Schröger, 2008; Elijah, Pelley, & Whitford, 2018; Mifsud et al., 2016; Neszmélyi & Horváth, 2017; Oestreich et al., 2016; van Elk et al., 2014; Pinheiro et al., 2019). The N1 is not a unitary component; in contrast, there are believed to be at least three obligatory sources for the N1 (Näätänen & Picton, 1987; Horváth, 2015). Given the observed scalp distribution and the long silent periods between trials (> 10 s on average), the present design may have tapped into the non-specific (i.e., modality free) N1 component (Davis & Zerlin, 1966; Hari et al., 1982; SanMiguel et al., 2013). N1 amplitude has been shown to index physical features of sound, notably auditory intensity (Beagley & Knight, 1967; Picton, Goodman, & Bryce, 1970; Adler & Adler, 1989). N1 suppression has been argued to reflect the sound of the *active* condition being processed as less intense than the *passive* condition, possibly through the action of efference copy / corollary discharge-related mechanisms (Hughes et al. 2013; Whitford, 2019). Previous research that manipulated the delay between action and effect found that delays longer than a few hundred milliseconds abolished the N1 suppression effect (Whitford et al., 2011; Oestreich et al., 2016; Pinheiro et al., 2019), suggesting that N1 suppression is dependent on the motor action occurring close-in-time to the resulting sound. The result of Experiments 1 and 2 corroborate this finding; the absence of N1-suppression in Experiment 1 suggests that a motor action is necessary for N1 suppression, while the absence of N1-suppression in Experiment 2 suggests that a motor-action must occur close-in-time to the resulting sound if it is to elicit N1-suppression. Our design attempted to control for motor-related differences and temporal predictability and control, which left participants' sense of agency as one of the few remaining differences between conditions. These results suggest that a motor action that is approximately temporally coincident with the sound is necessary for N1-suppression to occur, and that having a sense of agency over the sound is not sufficient. It is important to

note, however, that N1 amplitude can be influenced by factors other than the performance of willed motor actions. For example, several studies have shown that visual stimuli that are predictive of auditory events (such as an animation of a person clapping) can also result in a reduction in N1 amplitude. (Stekelenburg & Vroomen, 2007; Vroomen & Stekelenburg, 2010; Libesman, Mannion, & Whitford, 2020).

As indexed by the non-significant chi-squared tests, we did not find much evidence to suggest that participants varied in their choice frequencies for either experiment (i.e., the proportion of trials in which participants opted to hear vs. not hear the sound). However, if such a behavioural difference between conditions did in fact exist, then this would represent a potential confound that could underlie the apparent absence of N1-suppression in the two experiments.

The Tb component was suppressed in the *active* condition relative to the *passive* condition in both experiments. This suppression occurred in the absence of any motor action in Experiment 1, and when the motor-action was temporally distant and not time-locked to the sound in Experiment 2. Taken together, these results suggest that in contrast to N1, the Tb component, is sensitive to manipulations in sense of agency (i.e., the ability to cause the sound to occur), but is not dependent on the occurrence of a co-incident motor action, and thus is likely not dependent on efference copy / corollary discharge-related mechanisms. The Tb suppression effects observed in both experiments may have also received contribution from the relatively longer periods of silence between trials. SanMiguel et al. (2013) and Horváth (2013) also reported Tb suppression effects with long inter-stimulus intervals (ISI) (3.2 s and >4 s, respectively). SanMiguel et al. (2013) assessed Tb suppression among different levels of ISIs (0.8, 1.6 and 3.2s) but only reported Tb suppression effects with the longest ISIs.

The Tb component is believed to be generated within the secondary auditory cortex (Wolpaw & Penry, 1975; Gallinat et al., 2002; Tonnquist-Uhlen et al., 2003; Rihs et al., 2013), potentially in the vicinity of Wernicke's area (Alain, Woods, & Covarrubias, 1997). While the functional significance of the Tb component has not been definitively established, it has been implicated in auditory processing, particularly of 'high level' auditory stimuli including music and language (Giard et al., 1994; Tonnquist-Uhlen et al., 2003; Shahin, Bosnyak, Trainor, & Roberts, 2003; Langers, Backes, & van Dijk, 2007; Harpaz, Levkovitz & Lavidor, 2009; Hämäläinen et al., 2011; Bruneau et al., 2003; Azouz et al., 2014).

In regard to the present study: the results of both experiments indicated that Tb amplitude was decreased when participants had control over whether they heard the sound. In other words, the Tb component appeared to index participants' sense of agency over the sound. Our sense of agency has been argued to arise when our motor actions result in predictable sensory consequences (Blakemore et al., 2002; Synofzik et al. 2008). Given this, it may seem odd to divorce sense of agency from our motor actions. However, there are instances in real life where one may be in control of events by virtue of inaction; the classic trolley problem in philosophy is a theoretical example. A real-world example would be when one decides not to intervene when a jar is about to fall off a table. It may be helpful to distinguish between the *feeling of agency* versus the *judgement of agency*, as outlined by Synofzik et al. (2008). The *feeling of agency* is simply the sense of agency someone experiences when they perform a motor action that is followed by a sensory event. This is what the literature typically refers to when discussing agency within the context of comparator models (Synofzik et al., 2008). The *judgement of agency*, on the other hand, requires an explicit cognitive judgement of one's agency, and does not rely on sensorimotor indicators. The sense of agency experienced by participants in Experiments 1 and 2 would more likely be that of the *judgement of agency*, and it is therefore possible that it is

judgements of agency, as opposed to feelings of agency, that are indexed by Tb amplitude. This question has not (to our knowledge) been investigated previously and would be a worthwhile topic for future research. If the Tb component is found to index sense of agency (or even judgements of agency more specifically), it would be interesting to know whether Tb is specific to auditory stimuli, or whether analogous components can be elicited by manipulations of sense of agency in other sensory domains. However, it must be noted that it is uncommon for higher-order evaluative processes (such as cognitive judgements) to be associated with ERP components earlier than 300 ms. As such, it would be important for future research to further distinguish what processes contribute to the mediation of Tb amplitude.

The P2 component was enhanced in the *active* condition relative to the *passive* condition in Experiments 1 and 2. Although its functional significance is not clear, the P2 component has been associated with attention and categorization processes (García-Larrea, Lukaszewicz, & Mauguière, 1992; Crowley & Colrain, 2004; Lijffijt et al., 2009). Further evidence has also linked the P2 component to working memory processes (Lefebvre et al., 2005; Finnigan et al., 2011; Duzcu et al., 2019). Most studies investigating sensory attenuation have found suppression of the P2 component in the *active* condition relative to the *passive* condition (Knolle et al., 2012; Horváth & Burgyán, 2013; Timm et al., 2014; Klaffehn et al., 2019). However, the present study found P2 enhancement in the *active* condition. One potential reason for this inconsistency may be related to the long (> 1 s) and variable action-effect delays used in the present design. For example, Klaffehn et al. (2019) used a similar design (with a loading bar instead of a tickertape) in which there was a 750 ms delay between action and outcome. They observed no difference in P2 amplitude between the *active* and *passive* conditions; a result that is intermediate between the results of the present study (which had a longer action-effect delay and observed P2 enhancement) and most of the

existing literature (which has had negligible-to-small action-effect delays and observed P2 suppression). Another potential factor is sense of agency over the sounds. For example, a previous study by Timm, Schönwiesner, Schröger, and SanMiguel (2016) demonstrated significantly larger P2 amplitudes when participants experienced agency over sounds than when they did not. These results might suggest that the P2 and Tb components are suitable candidates for investigation of the relationship between the sense of agency and sensory attenuation.

It is also worth noting that N1 and P2 suppression effects are likely caused by different factors. For example, lesions to the cerebellum (thought to be a key anatomy of sensory attenuation (Knolle, Schröger, Baess & Kotz, 2012)), differentially affect N1- and P2- suppression, as does the type of motor-action (e.g., hand-movement vs foot-movement) producing the sensory outcome (van Elk et al., 2014). Though sensory attenuation studies have typically observed both N1- and P2- suppression in the *active* condition, the pattern of results for the P2 component has been less consistent than that of the N1 component (Pineiro et al., 2019). The results of the current study are consistent with previous research demonstrating higher P2 component amplitudes when stimuli are considered task relevant within working memory (Getzmann, Wascher, & Schneider, 2017; Duzcu et al., 2019). For Experiment 1, sounds produced in the *active* condition might have contained a novel relevance by virtue of the fact that it was inaction that caused the sound, since inactions rarely result in sensory consequences in everyday life.

There are several studies that have used similar designs to the present set of experiments. Weller et al. (2020) used a similar action/nonaction paradigm to assess temporal binding, a phenomenon wherein a voluntary action and a subsequent sensory effect are perceived to be temporally compressed (Haggard, Clark, & Kalogeras, 2002). The temporal compression of action and effect has been interpreted as an implicit marker of the sense of

agency. In Weller et al.'s (2020) second experiment, participants observed a rotating clock hand and were given the option to either press or not press a button in a given time frame. Both options produced distinct sounds. They then estimated the time between the point of action/inaction and sound onset. Weller et al. (2020) found that temporal binding effects existed even for inactions, thereby providing evidence that willed inactions can also result in a sense of agency. Their third experiment replicated the results of their second experiment but also controlled for temporal predictability. Here, participants used action/inaction to decide the direction that a pinball stimulus would fire a ball. When participants opted for inaction, a loading bar filled up, which was immediately followed by a clicking sound. After onset of the clicking sound, the ball would be fired from the pinball (which was paired with a ball launch sound). Participants were instructed to estimate the time interval between the clicking sound and the ball launch sound. Again, Weller et al. (2020) found a temporal binding effect for inactions, providing further evidence that willed inactions can result in a sense of agency. Participants in the third experiment also reported higher agency ratings for inaction compared to a baseline condition.

Another study by Klaffehn et al. (2019) assessed the role of sense of agency in the sensory attenuation effect. In this study, a loading bar was used to control for temporal predictability between the active and passive conditions. However, in contrast to the present study, they found evidence of N1 suppression effect for two of three electrodes (FCz and Cz) when a 750 ms delay was imposed between action and effect (similar to the present study in which the delay between action and effect was > 1 s). One possible explanation for why our N1 results are inconsistent with those of Klaffehn et al. (2019) may be the differences in ISI between experiments, as this may have led to the N1 waveform being dominated by different subcomponents. Klaffehn et al.'s (2019) study had ISIs of < 4 s, meaning that N1 waveforms may have been dominated by a frontal or fronto-central distribution (Vaughan & Ritter, 1970;

Horváth, 2015). In contrast, the present experiment included ISIs that were on average >10 s, meaning that the N1 was most likely dominated by the non-specific component. One possible future study to disentangle the inconsistent results may be to incorporate different ISIs within the same experiment, such as in the study of SanMiguel et al. (2013). Taken together, these results suggest that sensory attenuation may extend to action-effect pairings in which the participant has a sense of agency over a sensory outcome, but the action and outcome are not temporally coincident.

Several previous studies of sensory attenuation have linked the phenomenon with the characteristic abnormalities in agency that are often observed in patients with schizophrenia (e.g., Ford et al., 2001; Ford et al., 2007; Whitford, 2019). These models are often premised on the idea that sense of agency arises as a consequence of the same comparator processes that underlie sensory attenuation (Frith, Blakemore, & Wolpert, 2000). The alternative possibility is that sensory attenuation and sense of agency arise from distinct processes, and that schizophrenia is independently associated with deficits in both. By disambiguating the effects of motor action from sense of agency, our experimental paradigm may provide a platform for future studies aimed at disambiguating these competing possibilities, by testing whether schizophrenia patients show deficits in Tb suppression to controllable sounds arise as a consequence of willed inactions.

In conclusion, the results of this study suggest that motor-actions and sense of agency have differential effects on the evoked response to self-initiated sounds, and are indexed by different components of the auditory evoked potential. Specifically, while N1-suppression did not occur in the absence of a temporally coincident motor action, Tb-suppression did occur when participants could control whether or not a sound was presented by means of a willed inaction. This result suggests that the Tb component may index one's sense of agency over

sensory events. Whether this role is limited to auditory events or extends to other sensory modalities is an open question, and may be a worthwhile question for future research.

Chapter 3: Investigating the role of contingency on neurophysiological indices of sense of agency

3. 1. Preamble

In Chapter 2, we introduced a novel experimental paradigm that attempted to disentangle the effects of motor actions and sense of agency when investigating the phenomenon of sensory attenuation. In the experiments of the previous chapter, participants generated sounds either via a willed inaction (Experiment 1) or by a button-press that was temporally divorced from the sound (Experiment 2). In both experiments, we did not observe any effect of N1 suppression, suggesting that N1-suppression is dependent on a close temporal congruence between action and sound. However, we observed effects of Tb suppression and P2 enhancement in both experiments. These results suggest that motor-actions and the sense of agency can have differential effects on sensory attenuation and may be indexed by different components of the ERP. More specifically, the results suggest that the Tb component, and possibly the P2 component, are good candidates for representing the effects of variations in sense of agency on sensory attenuation. In contrast, the results suggest that N1 suppression is tied to the presence of a motor-action that is temporally locked to the sound itself.

The aim of the present chapter is to investigate the effects of contingency—operationalized in terms of the probability of a sound occurring because of a willed action or inaction — on sensory attenuation. Contingency—when operationalized in terms of probability— is an area that is largely unexplored within the field of sensory attenuation. An advantage of our experimental paradigm is that it can be adapted to investigate effects of contingency by manipulating the probability of sound onset. In the present series of experiments, participants again elicited sounds via willed inactions (Experiment 3) or a button-press that was temporally dissociated from the sound (Experiment 4). Sounds

followed these willed actions or inactions either 100% of the time (*Full Contingency*, or *FC* condition) or 50% of the time (*Half Contingency*, or *HC* conditions). Based on the results of the previous chapter, effects of contingency are expected to be mediated by the Tb component, rather than the N1 component. This is because, as demonstrated in the previous chapter, Tb amplitude is likely to be modulated by the participant's sense of agency. As I expect participants to experience a greater sense of agency when sensory contingency is 100% rather than 50%, I anticipate Tb amplitudes to be smaller when contingencies are at 100% relative to when contingency is set at 50%.

3. 2. Abstract

Stimuli that have been generated by a person's own willed motor actions generally elicit a suppressed neurophysiological, as well as phenomenological, response than identical stimuli that have been externally generated. This well-studied phenomenon, known as sensory attenuation, has mostly been studied by comparing ERPs evoked by self-initiated and externally generated sounds. However, most studies have assumed a uniform action-effect contingency, in which a motor action leads to a resulting sensation 100% of the time. In this chapter, we investigated the effect of manipulating the probability of action-effect contingencies (*contingency*) on the sensory attenuation effect. In Experiment 3, participants watched a moving, marked tickertape while EEG was recorded. In the *Full Contingency (FC)* condition, participants chose whether to press a button by a certain mark on the tickertape. If a button-press had not occurred by the mark, a sound would be played a second later 100% of the time. If the button was pressed prior to the mark, the sound was not played. In the *Half Contingency (HC)* condition, participants observed the same tickertape; in contrast, however, if participants did not press the button by the mark, a sound would occur only 50% of the time (*HC-inaction*). Furthermore, in the *HC* condition, if a participant pressed the button

prior to the mark, a sound would also play 50% of the time (*HC-action*). In Experiment 4, the design was identical, except that a willed action (as opposed to a willed inaction) triggered the sound in the *FC* condition. The results were consistent across the two experiments: while there were no differences in N1 amplitude between conditions, the amplitude of the Tb component was smaller in the *FC* condition when compared to the *HC-inaction* condition. The amplitude of the P2 component was also smaller in the *FC* condition compared to both the *HC-action* and *HC-inaction* conditions. The results suggest that the effect of *contingency* on neurophysiological indices of sensory attenuation may be indexed primarily by the P2 and Tb components, rather than the N1 component which is most commonly studied.

3. 3. Introduction

The experiments in the previous chapter indicated that participants' motor actions *per se* and their sense of agency have differential effects on sensory attenuation to sounds and may be indexed with different ERP components. To accomplish this, we developed a novel adaptation of the classical self-stimulation paradigm, wherein participants, rather than performing a time-locked motor action, instead made a decision (that was not time-locked to the sound) in order to trigger the auditory stimulus. The results revealed that N1 suppression did not occur in the absence of a motor action time-locked to the sound, suggesting that N1-suppression may be underpinned primarily by motor-based predictions. In contrast, the observed suppression of the Tb component in the active condition, even in the absence of a simultaneous motor-action, suggests that the Tb component may be sensitive to between-condition differences in sense of agency.

Our novel paradigm has the potential to test a variety of different phenomena related to sensory attenuation, particularly for situations in which participants' motor-actions are dissociated from their sense of agency. One topic that has remained largely unexplored in this space is the role of stimulus contingency. Here, we define contingency as the probability of a stimulus (in this case, a sound) occurring as a result of a willed action (or willed inaction). Although there have been some attempts to investigate contingency in the sensory attenuation literature, most previous studies have operationalised contingency in terms of temporal contingency; specifically, most previous studies have manipulated contingency by varying the temporal delay between the motor action and sound. For example, Bäß, Jacobsen, and Schröger (2008) investigated the effect of tone frequency and onset predictability on N1 suppression. In their *motor-auditory* and *auditory-only* conditions, frequency and onset predictability were manipulated in a 2x2 design. Sounds could be (a) predictable in both frequency (a 1000 Hz sound) and onset, in which the sound immediately followed the button

press, (b) unpredictable in frequency (ranging from 400 to 1990 Hz) but predictable in onset, (c) predictable in frequency but unpredictable in onset, in which a random delay of 500 to 1000 ms was imposed between the action and effect, (d) unpredictable in both frequency and sound onset. They found that N1 suppression occurred regardless of the predictability of the frequency and onset of the sound. Pinheiro, Schwartz, Gutierrez, and Kotz (2019) conducted a study where various delays were inserted between the action and sound within action-effect contingencies as to induce temporal prediction errors. In 30% of trials, sounds that followed the button-press were presented with a delay of either 50 ms, 100 ms, or 250 ms. They found that N1 suppression still occurred with delays of up to 100 ms between the action and the sound.

Another method of manipulating contingency is by changing the probability of a sound occurring as a result of the action. Typical self-stimulation experiments often have action-effect contingencies of 100%, meaning that actions (e.g., button-presses) lead to sounds in 100% of trials (Horvath, 2015). Action-effect contingencies— in ecological settings— do not always occur in the uniform manner that they do in the laboratory setting. People sometimes incorrectly predict the outcome of an action (for example, when trying to guess the outcome of a button-press on a slots machine). Essentially, manipulation of action-effect contingency is a method of modifying participants' confidence in their predictions regarding the sensory consequences of their actions. In essence, both forms of operationalization— by which we mean both manipulating of temporal onset versus the manipulating the probability of sounds occurring— perform the function of reducing the participant's confidence that the expected sensory event will occur.

The following series of experiments used a modified version of the experimental paradigm introduced in Chapter 2 to explore the impact that manipulating action-effect contingency had on the phenomenon of sensory attenuation. In this chapter, the action-effect

contingency was manipulated by varying the probability that the button-presses would result in a tone being played. In these two experiments, participants observed a short animation and on each trial were required to decide whether or not to press the button. In both experiments, there were two conditions: the *Full-Contingency* condition (FC) and the *Half-Contingency* condition (HC). In the FC condition, sounds *always* followed the inaction (in Experiment 3), or *always* followed the action (in Experiment 4). In contrast, sounds followed the inaction (Experiment 3) or action (Experiment 4) only 50% of the time in the HC condition.

Like most previous studies in the sensory attenuation literature, we analysed the N1 and P2 components of the ERP. We also included the Tb component, which is believed to reflect activity of the secondary auditory cortex (Wolpaw & Penry, 1975; Gallinat et al., 2002; Tonnquist-Uhlen et al., 2003; Rihs et al., 2013), and which we have previously found (in Chapter 2) to be associated with participants' sense of agency over the sound. Previous research using the 'traditional' self-stimulation paradigm has demonstrated suppression across the N1, Tb, and P2 components in the *active* condition relative to the *passive* condition (Knolle et al., 2012; SanMiguel, Todd, & Schröger, 2013). However, given that our studies use a different methodology compared to the traditional self-stimulation paradigm (Schafer & Marcus, 1973), we do not expect to find any evidence of N1-suppression in this study. This hypothesis was based on the based on the results of Chapter 2, and the fact that our paradigm had clear temporal discrepancy between the action and effect. Instead, based on the results of the previous chapter, effects of contingency are expected to be mediated by the Tb component. This is because, as demonstrated in the previous chapter, Tb amplitude is likely to be modulated by the participant's sense of agency. As I expect participants to experience a greater sense of agency when sensory contingency is 100% rather than 50%, I hypothesise that Tb amplitudes will be smaller when contingencies are at 100% relative to when contingency is set at 50%.

3. 4. Method

3. 4. 1. Experiment 1

3. 4. 1. 1. Participants

Forty undergraduate students from the University of New South Wales (Sydney, Australia) participated in the study in exchange for course credit ($n = 40$). All participants gave written informed consent prior to the experiment. Two participants were removed from analysis due to insufficient number of artifact-free epochs (as described in *EEG Recording and Analysis*) leaving a final sample of $n = 38$ participants (mean age = 21 years, $SD = 7.5$, 16 females). The study was approved by the Human Research Ethics Advisory Panel (Psychology) at the University of New South Wales.

3. 4. 1. 2. Stimuli, Materials, and Procedure

The audio stimulus was a sinusoid tone of frequency 1000 Hz, 100 ms duration, with a 5 ms linear rise/fall time. Audio stimuli were sent to participants through Sennheiser HD 210 headphones. Audio input/output was controlled by a specially written MATLAB script and was delivered via an AudioFile Stimulus Processor (Cambridge Research Systems). Participants made responses by pressing the space bar of a low-latency keyboard (DuckyShine 4, 1000 Hz report rate). Visual stimuli were displayed on a high-performance 24-inch monitor (BenQ XL2420T).

During each trial, participants observed a visual animation; the animation was the same as described in the Chapter 2 experiments. The animation lasted for about 6 seconds. A schematic of the animation is presented in Figure 1. The animation consisted of a central red fixation line that sat in the middle of a green horizontal bar, which is referred to as the ticker tape. Participants were instructed to keep their eyes fixated on the fixation line during the trial. There was also a blue ‘decision line’ and a green ‘trigger line’ located on the right side

of the ticker tape. The trigger line was initially positioned on the far right-hand side of the ticker tape; the decision line sat to the left of the trigger line (Figure 1A).

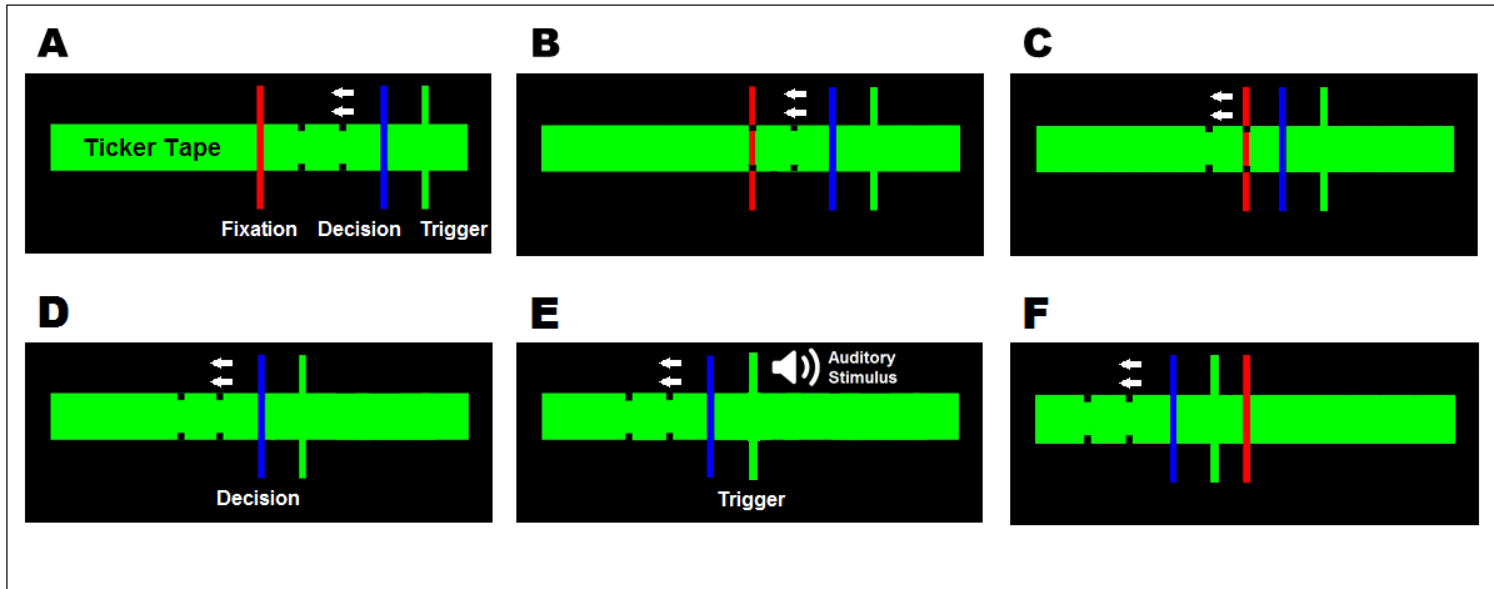


Figure 3. 1. A schematic of the experimental protocol. Participants were instructed to fixate their eyes on the central red fixation line (Panel A). After a one second delay, the blue decision line and the green trigger line moved slowly towards the central red fixation line at a rate of 6.5 degrees per second (Panel B-C). Participants were told that they had the option of pressing the space bar of the keyboard by the decision time (Panel D). In the *FC* condition in Experiment 3, if the participant pressed the space bar before the decision line overlapped with the fixation line, this would cause the audio stimulus to be played at trigger time (Panel E). If the participant did not press the space bar during this time frame, the audio stimulus would not play at the trigger time. In the *FC* condition in Experiment 4, this contingency was reversed, such that if participants pressed the space bar before the decision time, this would inhibit the audio stimulus from being played at the trigger time. Vice versa, if participants did not press the space bar during this time frame, this would cause the audio stimulus to be played at the trigger time. In the *HC* condition in both Experiment 3 and 4, the contingencies were set so that audio onset would only follow button presses 50% of the time. Vice versa, audio onset would also occur to inaction 50% of the time. Participants were not told that the probability in the *HC* condition was 50% but were told that sounds “may or may not be played”. The lines continued to move for another 1 s, before the animation concluded and the trial concluded, and the trial was completed (Panel F)

Upon commencement of the trial, after a one second delay, both the decision line and the trigger line started to move towards the fixation line at a constant rate of 6.5 degrees per second. The decision line intersected the fixation line after approximately 3 seconds. The trigger line intersected the fixation line after approximately 4 seconds; at this point, the auditory stimulus was presented (depending on the trial, as described below). The lines continued to move for another 1 second, before the trial was completed.

There were two conditions in the experiment: the *Full-Contingency (FC)* condition and the *Half-Contingency (HC)* condition. In the *FC* condition, participants had the option of pressing the space bar on the keyboard before the decision line intersected the fixation line (hereon referred to as the ‘decision time’). Participants were told that if they did not press the button by the decision time (*Figure 1B*) – i.e., if they performed a willed inaction – this would cause the audio stimulus to be played at the exact moment that the trigger line intersected the fixation line (hereon referred to as the ‘trigger time’) (*Figure 1C*). If they chose to press the space bar before the decision time, this prevented the audio stimulus from being played at the trigger time. The contingencies were set so that inaction would *always* cause the audio stimulus to be played at the trigger time; conversely, pressing the button would always cause no sound to be played at the trigger time. Participants were asked to press the space bar on approximately half the trials while trying not to conform to an obvious pattern of responses. At the start of every trial, participants were reminded (by means of instructions on the screen) as to what their options were, and what the consequences would be.

In the *HC* condition, participants were given instructions that were nearly identical to the instructions in the *FC* condition. However, the contingencies were set so that audio onset would only follow button presses 50% of the time. Conversely, audio onset would also occur to inaction 50% of the time. Essentially, whether the participant did or did not hear a sound

during any given trial was random. Participants were not told of the exact contingencies but were instead told that sounds “*may or may not*” occur as a result of their actions in the instructions.

The experiment consisted of five *FC* blocks and ten *HC* blocks, totaling 15 blocks for the whole experiment. For ease of reference within Experiment 3, we make the following distinction between three different trial-types:

- *FC* trials: in which participant inactions resulted in a sound 100% of the time
- *HC-action* trials in which participant action resulted in a sound 50% of the time
- *HC-inaction* trials in which participant inaction resulted in a sound 50% of the time. It is important to note that *HC-action* and *HC-inaction* -trials occurred within the same block

There were twice the number of *HC* blocks compared to *FC* blocks in the experiment. This was done in order to achieve approximately equal number of usable epochs, given that the sound was only presented on approximately 50% of trials in the *HC* condition. Furthermore, *FC* blocks that used button-presses to trigger sounds were not included and were instead used as the basis of Experiment 4 because that would result in doubling the amount of *FC* blocks, causing the experiment to be too long. Only trials in which the auditory stimulus were played were analyzed. Each block contained 24 trials. The order of the blocks alternated between the *FC* and *HC* blocks so that there were two *HC* blocks for every one *FC* block. Within the grouping of three blocks (two *HC* blocks and one *FC* block), the order was counterbalanced between participants. The starting block was also counterbalanced between participants.

3. 4. 1. 3. EEG Recording and Analysis

EEG was recorded with a BioSemi ActiveTwo system from 64 Ag/EgCl active electrodes (*P1, FPz, FP2, AF7, AF3, AFz, AF4, AF8, F7, F5,F3, F1, Fz, F2, F4, F6, F8, FT7, FC5, FC3, FC1, FCz, FC2, FC4, FC6, FT8,T7, C5, C3, C1, Cz, C2, C4, C6, T8, TP7, CP5, CP3, CP1, CPz, CP2, CP4,CP6, TP8, P9, P7, P5, P3, P1, Pz, P2, P4, P6, P8, P10, PO7, PO3, POz,PO4, PO8, O1, Oz, O2, Iz*). A vertical electrooculogram (EOG) was recorded by placing an electrode above and below the left eye; a horizontal EOG was recorded by placing an electrode on the outer canthus of each eye. Electrodes were also placed on each mastoid, and the nose. During data acquisition, the reference was composed of sites CMS and DRL, and the sampling rate was 2,048 Hz.

For data analyses, we re-referenced the EEG data offline to the nose electrode, as is common in studies investigating the components-of-interest, and necessary for extracting the Tb component (Näätänen & Picton, 1987; SanMiguel et al., 2013; Woods, 1995). Data were band-pass filtered from 0.1 to 30 Hz using a half-amplitude phase-shift-free Butterworth filter, then notch filtered (50Hz) to remove mains artefact. The filtered data were segmented into 500 ms epochs, from -100 ms pre-stimulus to 400 ms post-stimulus. Only trials in which the auditory stimulus were played were analyzed. Epochs were baseline-corrected to the mean voltage from -100 to 0 ms. We corrected the epochs for eye blinks and movement artefacts using the technique described in Gratton, Coles, and Donchin (1983) and Miller, Gratton, and Yee (1988). We excluded all epochs with signals exceeding peak-to-peak amplitudes of 200 uV and had a maximal allowed voltage step of 50 uV/ms. We analysed the amplitudes of the N1, Tb and P2 components of the auditory-evoked potential, which were calculated as the average voltage within time-windows (30 ms width), the centers of which were defined using the collapsed localiser approach (Luck & Gaspelin, 2017). The collapsed localiser approach is a technique whereby one first averages (or ‘collapses’) the ERP

waveforms across all conditions for all participants. The components-of-interest (e.g., N1, Tb, P2) are identified on this ‘collapsed’ waveform, and a time-window is centred around these peaks, which is then used for the statistical analysis of the original (or ‘uncollapsed’) waveforms (Luck & Gaspelin, 2017).

For the N1, Tb, and P2 components, mean voltage in the analysis window was submitted to paired samples t-tests. For each component, there were two contrasts of interest (1) *FC* versus *HC-action* and (2) *FC* versus *HC-inaction*. Electrodes of interest for the N1 component were Fz, FCz, and Cz, while the electrodes of interest for the P2 component were FCz, Cz, and CPz. For the N1 and P2 components, electrodes and analyses were chosen to be consistent with Whitford et al. (2017) and Jack et al. (2019) and were also centred around the electrode for which the signal was maximal (i.e., FCz for the N1 component and Cz for the P2 component). Although the electrode selection for the N1 and P2 components would have benefited from being identical to that of Chapter 2, as that would have allowed for a more direct comparison of the results, this was not possible because the manuscript reviewer for Chapter 2 had asked for the electrode selection for the N1 and P2 components to be expanded. Electrodes for the Tb component (T7 and T8) were based on recommendations by Tonnquist-Uhlen et al. (2013) and SanMiguel et al. (2013).

3. 4. 1. 4. Experiment 3 Results

The results of Experiment 3 are illustrated in Figure 4. There was an average of 58.5 (SD = 7.1) usable epochs in the *FC* condition, 57.2 (SD = 7.4) in the *HC-inaction* condition, and 59.8 (SD = 6.9) in the *HC-action* condition. If a participant pressed the button on exactly half the trials in the *FC* condition, and if all epochs were artefact-free, there would be 60 usable epochs in the *FC* condition. Likewise, if participants followed instructions perfectly, and if all epochs were artefact-free, there would be 60 usable epochs in the *HC* condition when triggered by inaction and 60 usable epochs in the *HC* condition when triggered by a

button press. Choice frequencies (i.e., the proportion of trials in which participants heard the sound) were obtained for the *FC* and *HC* conditions. Participants' choice frequencies in the *FC* condition were 61.3 sound trials (SD = 4.9), 60.8 sound trials in the *HC-inaction* condition (SD = 6.9), and 62.4 sound trials in the *HC-action* condition (SD = 6.7).

N1

Figure 2A shows the grand average N1 component elicited in the *FC* and *HC* conditions. The time-window for the N1 analysis was 109.5 – 139.5 ms. The contrast comparing *FC* vs. *HC-inaction* did not reach significance, $t(37) = 1.769$, $p = .085$. Similarly, the contrast comparing *FC* vs. *HC-action* also did not reach significance, $t(37) = -.336$, $p = .739$. These results indicate that the N1 amplitude did not differ between the *FC* and *HC* conditions, regardless of whether the sounds in the *HC* condition were associated with an inaction or a button-press.

Tb

Figure 2B shows the Tb component analysis elicited in the *FC* and *HC* conditions. The time-window for the Tb analysis was 122.2 – 152.2 ms. The contrast comparing *FC* vs. *HC-inaction* reached significance, $t(37) = 2.586$, $p = .014$ while the contrast comparing *FC* vs. *HC-action* did not reach significance, $t(37) = 1.162$, $p = .253$. The results indicate that the Tb amplitude of the *FC* condition was suppressed relative to the amplitude of the *HC* condition, but only in the case where sounds in the *HC* condition were elicited via inaction. However, Tb amplitude in the *FC* condition did not differ from Tb amplitude in the *HC* condition when sounds in the *HC* condition were elicited by button-press.

P2

Figure 2C shows the P2 component analysis elicited in the *FC* and *HC* conditions. The time-window for the P2 analysis was 224.7 – 254.7 ms. The contrast comparing *FC* vs. *HC-inaction* was highly significant, $t(37) = -3.523$, $p = .001$ as was the contrast comparing *FC* vs.

HC-action , $t(37) = -3.447$, $p = .001$. The results indicate that the P2 amplitude of the *FC* condition was strongly suppressed relative to the amplitude in the *HC* condition both when sounds in the *HC* condition were elicited by button-press, or when they were elicited via a willed inaction.

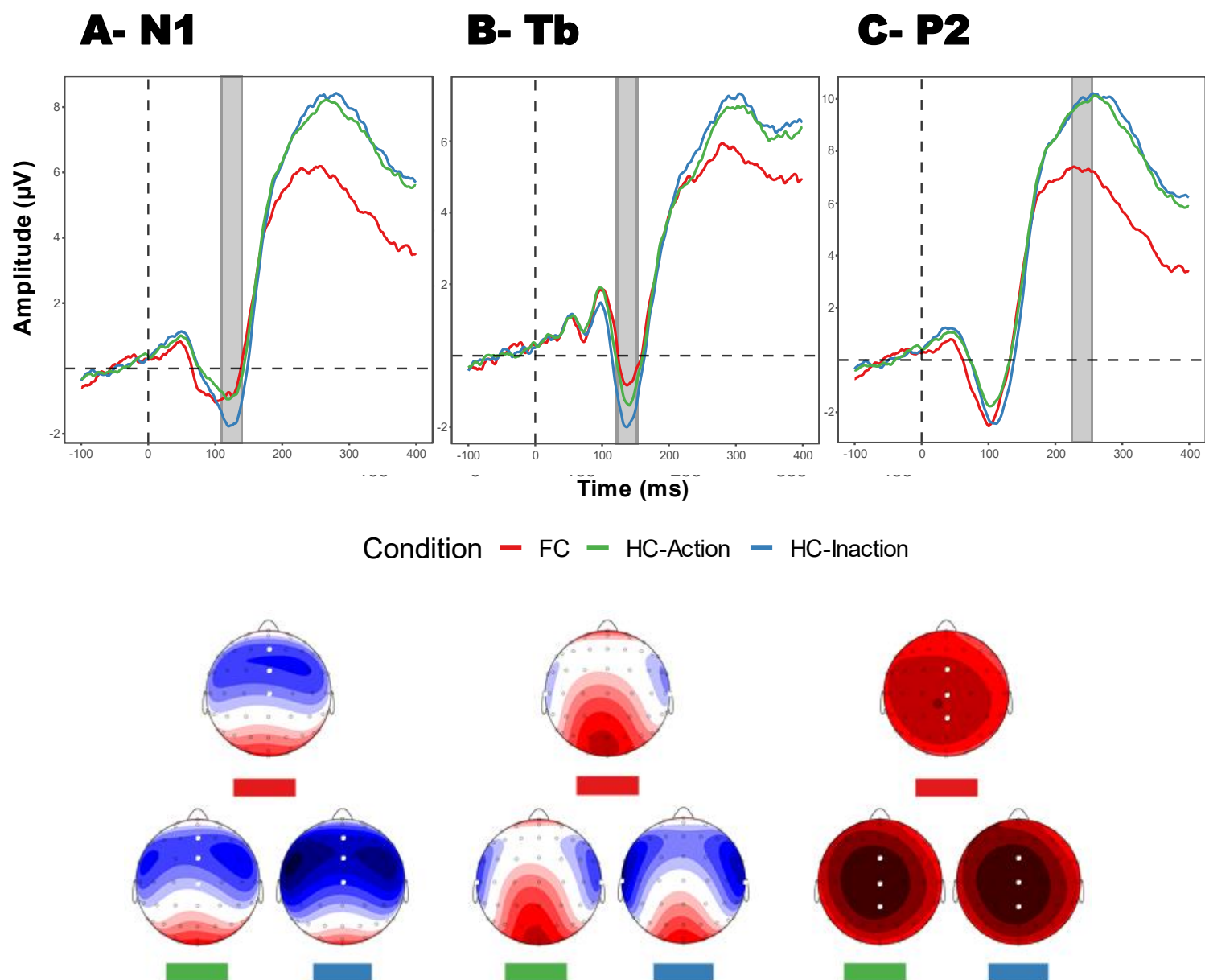
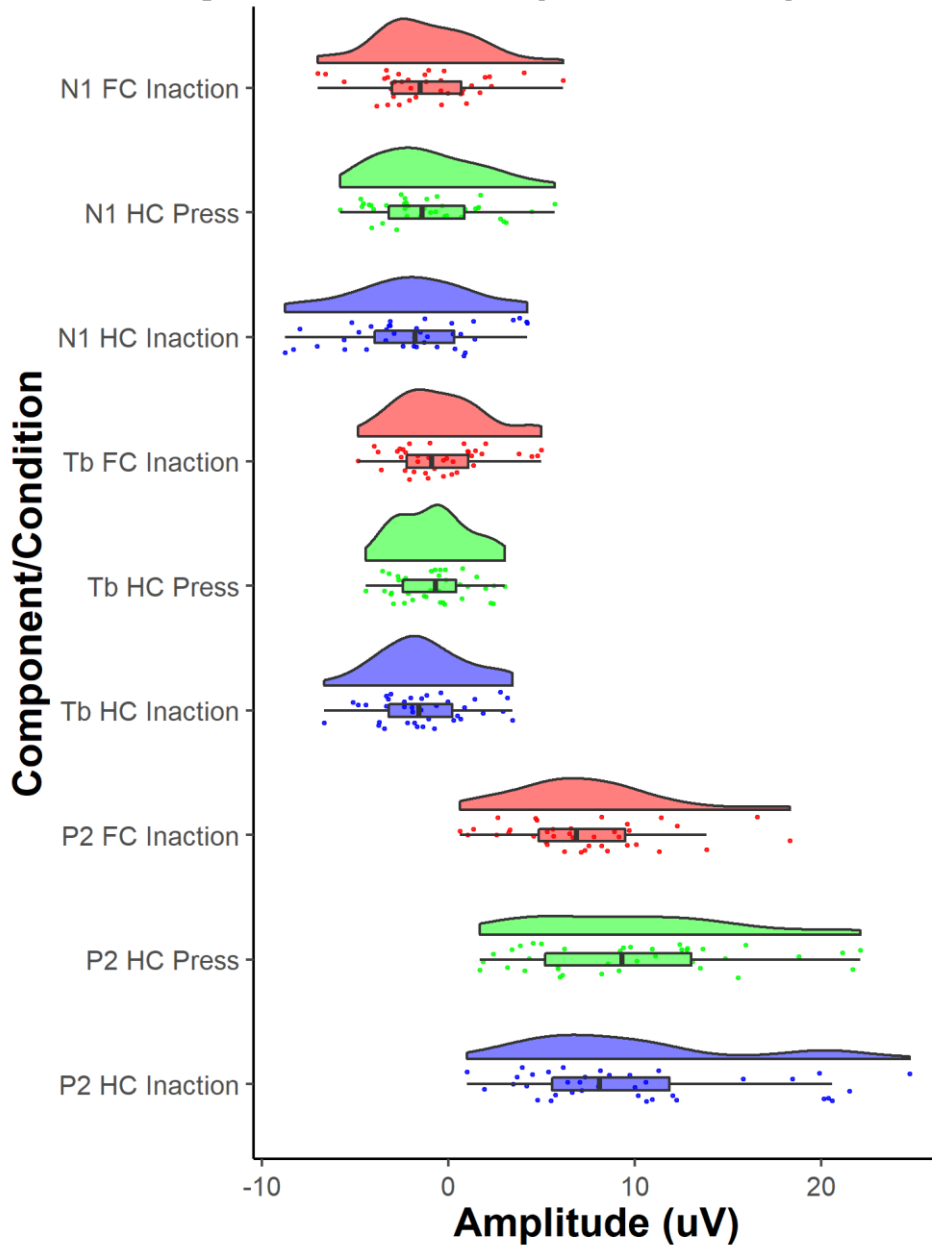


Figure 3. 2. Experiment 3: Waveforms showing ERPs elicited by the FC condition and the HC-action and HC-inaction conditions in addition to corresponding topographic mappings. White dots illustrate the electrodes used in the analysis. (A) The N1 component was measured at electrodes Fz, FCz, Cz, with time-window 85.6 – 115.6 ms. (B) The Tb component was measured at electrodes T7 and T8, with time-window 133.9 – 163.9 ms. (C) The P2 component was measured at electrodes FCz, Cz, CPz, with time-window 183.7- 213.7 ms. (D) Raincloud graph containing density plots and scatter plots of mean amplitudes for the N1, Tb, and P2 components for the FC and HC conditions (below next page).

Experiment 3 (Inaction)



3. 4. 1. 5. Experiment 3 Discussion

In Experiment 3, participants completed a variation of the traditional self-stimulation task in which the sound was not time-locked to a motor action. In the *FC* condition, participants were instructed that choosing *not* to perform an action by the ‘decision time’ would cause a sound to be played at the subsequent ‘trigger time’. In the *HC* condition, participants were given the same choice, but action-effect contingencies were set at 50%

rather than 100%, meaning that the probability under which sounds occurred was only 50% following a participant choice. That is, in the HC condition, electing not to press a button (*HC-inaction*) led to a sound on 50% of trials, while electing to press the button (*HC-action*) also led to the sound being presented on 50% of trials. The results revealed that the amplitude of the N1 components did not differ between the *FC* and *HC* conditions. The amplitudes of the Tb condition did differ, with Tb suppressed in the *FC* condition relative to the *HC-inaction* condition, but not the *HC-action* condition. The P2 component in the *FC* condition was strongly suppressed relative to both the *HC-inaction* and *HC-action* conditions.

In Experiment 3, participants were instructed that the performance of a willed inaction would elicit a sound in the *FC* condition. They were also instructed that a willed inaction “*may or may not*” cause a sound to be played in the *HC-inaction* condition. The aim of Experiment 4 was to investigate whether the key results of Experiment 3 (i.e., suppression of the Tb and P2 components in the *FC* condition relative to the *HC* conditions) would be replicated if the instructions were reversed i.e., if participants were instructed that the performance of a willed action (button-press) would elicit a sound in the *FC* condition.

3. 4. 2. Experiment 4

3. 4. 2. 1. Participants

Forty-nine undergraduate students from the University of New South Wales (Sydney, Australia) participated in the study in exchange for course credit. All participants gave written informed consent prior to the experiment. Four participants were removed from analysis due to insufficient number of artifact-free epochs (as described in *EEG Recording and Analysis*) leaving a final sample of $n = 45$ participants (mean age = 19 years, $SD = 1.8$, 24 females). The study was approved by the Human Research Ethics Advisory Panel (Psychology) at the University of New South Wales.

3. 4. 2. 2. Stimuli, Materials, and Procedure

The stimuli and materials were identical to Experiment 3. The only difference between the experiments was the action-effect contingency in the *FC* condition. Specifically, in Experiment 3, the audio stimulus was played if the participant opted *not* to press the button before the decision time, and participants were informed of this fact. In Experiment 4, this contingency was reversed: the audio stimulus was played *if and only if* the participant elected to press the button prior to the decision time, and participants were informed of this fact. As in Experiment 3, the audio stimulus was played at the trigger time, which occurred 1 s after the decision-time. There was no change to the instructions in the *HC* condition.

3. 4. 2. 3. EEG Recording and Analysis

The EEG recording and analysis were identical to Experiment 3.

3. 4. 2. 4. Experiment 4 Results

There was an average of 60.3 (SD = 5.4) usable epochs in the *FC* condition, 60.3 (SD = 7.1) in the *HC* condition when triggered by a button press, and 54.8 (SD = 7.2) in the *HC* condition when triggered by inaction. If a participant pressed the button on exactly half the trials in the *FC* condition, and if all epochs were artefact-free, there would be 60² usable epochs in the *FC* condition. Likewise, if participants followed instructions perfectly, and if all epochs were artefact-free, there would be 60 usable epochs in the *HC* condition when triggered by a button press and 60 usable epochs in the *HC* condition when triggered by inaction. Participants' choice frequencies in the *FC* condition were 62.4 sound trials (SD = 4.4), 62.8 sound trials in the *HC-action* condition (SD = 6.4), and 57.3 sound trials in the *HC-inaction* condition (SD = 6.0).

² Although there ought to be up to 60 usable epochs, there were on average 60.3 usable epochs in the *FC* condition and *HC-action* condition. This is because there were several instances when the MATLAB program running the experiment crashed, causing a restart on the current experimental block. This contributed to the extra trials through the experiment.

N1

Figure 3A shows the N1 component analysis elicited in the *FC* and *HC* conditions. The time-window for the N1 analysis was 85.6 – 115.6 ms. The contrast comparing *FC* vs. *HC-action* did not reach significance, $t(44) = -1.102$, $p = .276$. Similarly, the contrast comparing *FC* vs. *HC-inaction* did not reach significance, $t(44) = -1.766$, $p = .084$.

Tb

Figure 3B shows the Tb component analysis elicited in the *FC* and *HC* conditions. The time-window for the Tb analysis was 175.9 – 205.9 ms. The contrast comparing *FC* vs. *HC-action* did not reach significance, $t(44) = .801$, $p = .427$. However, the contrast comparing *FC* vs. *HC-inaction* was statistically significant, $t(44) = 2.126$, $p = .039$, with the *HC-inaction* condition showing a larger Tb amplitude than the *FC* condition.

P2

Figure 3C shows the P2 component analysis elicited in the *FC* and *HC* conditions. The time-window for the P2 analysis was 183.7 – 213.7 ms. The contrast comparing *FC* vs. *HC-action* reached significance, $t(44) = -2.208$, $p = .032$. Similarly, the contrast comparing *FC* vs. *HC-inaction* also reached significance, $t(44) = -3.305$, $p = .002$.

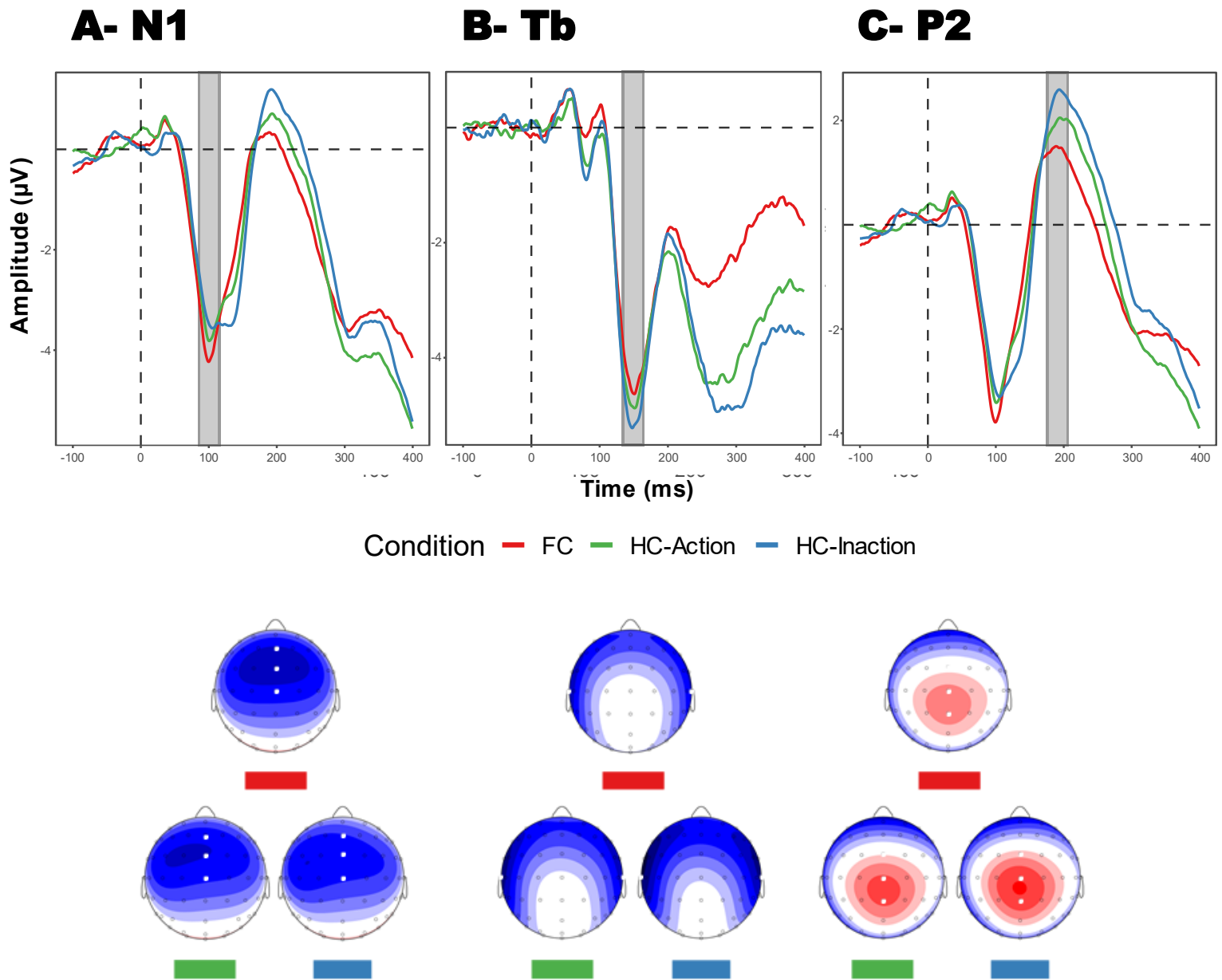
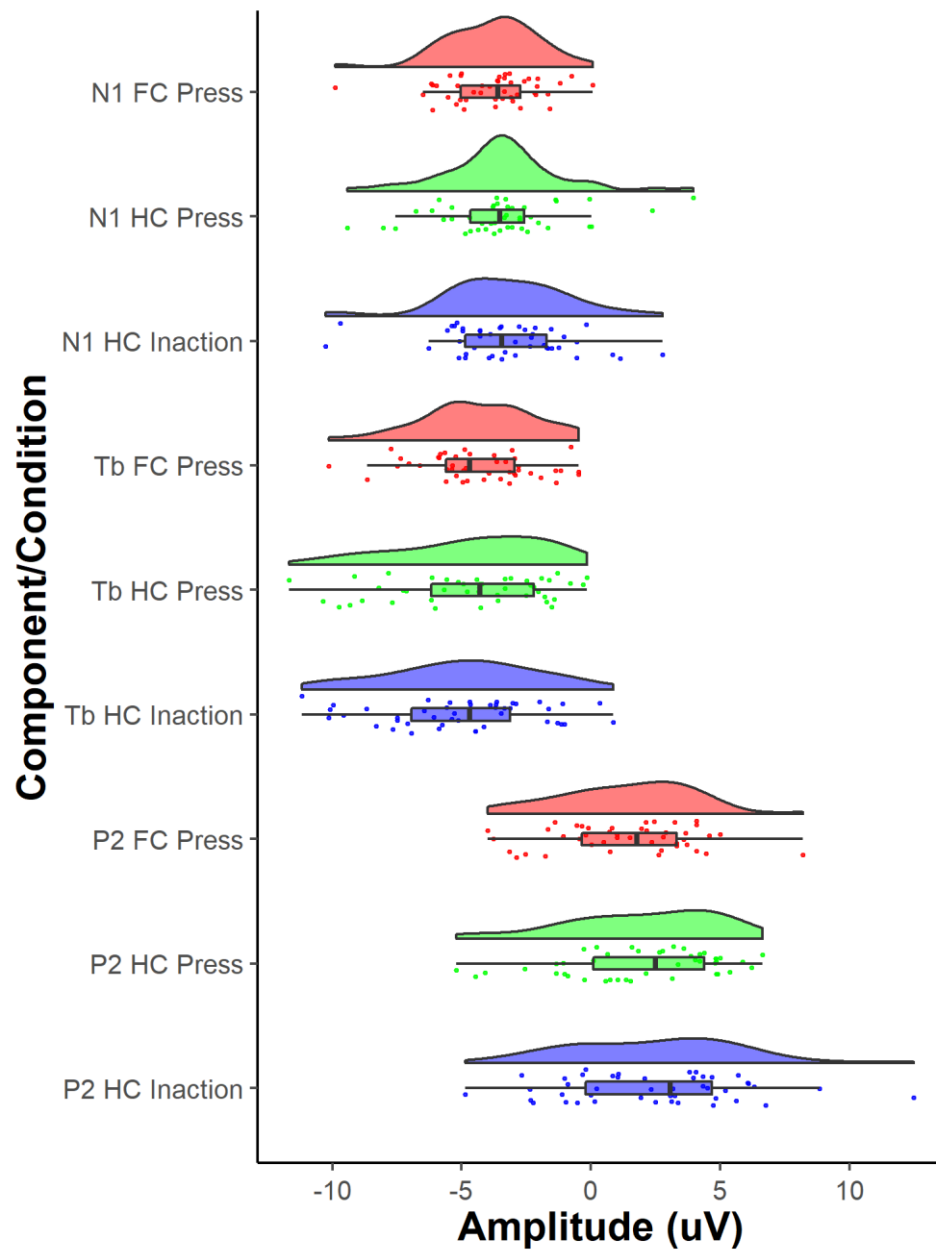


Figure 3.3. Experiment 4: Waveforms showing ERPs elicited by the *FC* condition and the *HC-action* and *HC-inaction* conditions, and the corresponding topographic mappings. White dots illustrate the electrodes used in the analysis. (A) The N1 component was measured at electrodes Fz, FCz, Cz, with time-window 85.6 – 115.6 ms. (B) The Tb component was measured at electrodes T7, T8, with time-window 133.9 – 163.9 ms. (C) The P2 component was measured at electrodes FCz, Cz, CPz, with time-window 175.9- 205.9 ms. (D) Raincloud graph containing density plots and scatter plots of mean amplitudes for the N1, Tb, and P2 components for the *FC* and *HC* conditions (below).

Experiment 4 (Action)



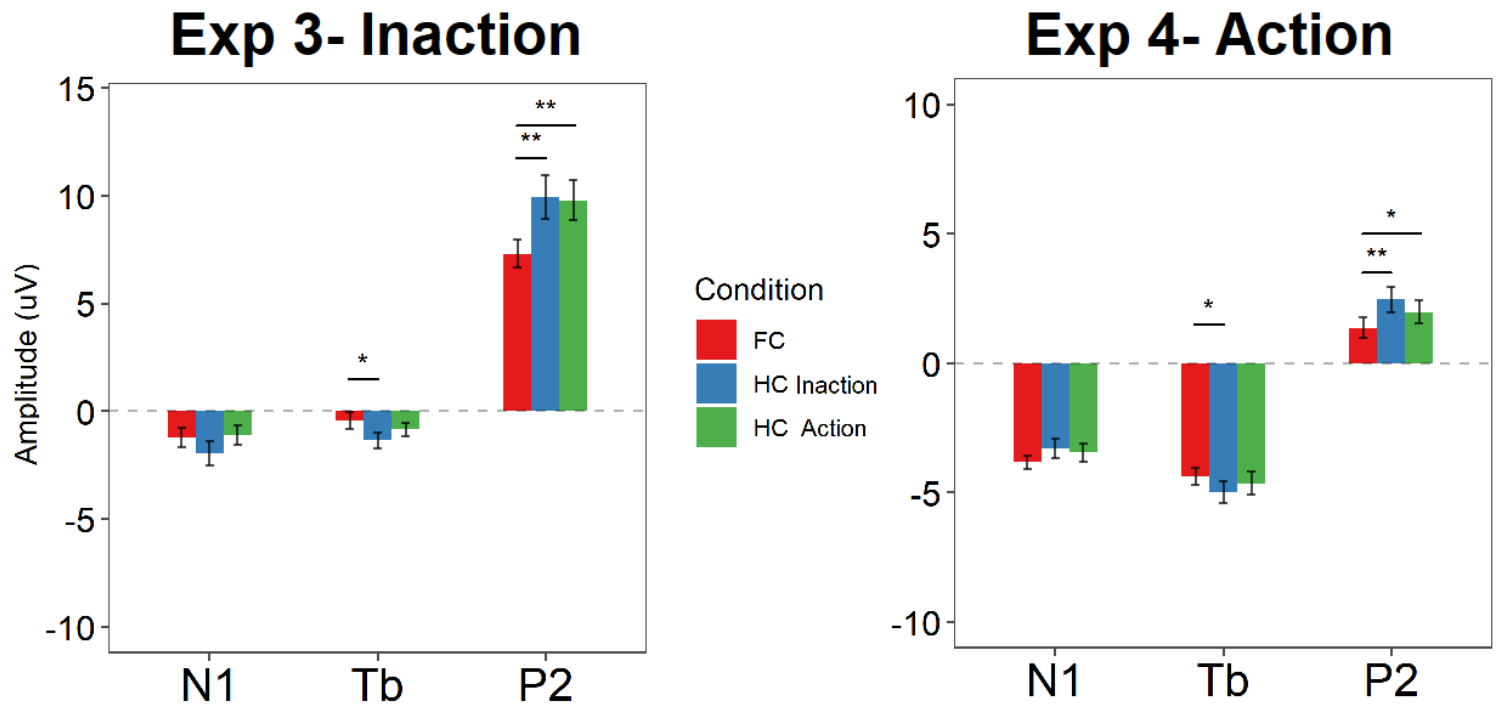


Figure 3. 4. Bar graphs of Experiments 3 and 4 illustrating mean amplitudes for the N1, Tb, and P2 components for the *FC* and *HC* conditions. Error bars show the standard error of the mean (SEM). Asterisks represent levels of significance (* $p < 0.05$; ** $p < 0.01$).

3. 5. General Discussion

The results of both experiments are summarized in Figure 4. In the current study, participants were required to either performed a willed *inaction* (in Experiment 3) or a willed *action* (a button-press, in Experiment 4) in order for a sound to be played a second or more later. Participants' neurophysiological response to the sound was then measured with EEG. The pattern of results was identical across the two experiments. N1 amplitudes did not differ significantly across the *FC* condition and *HC* condition, whether triggered by inaction (*HC-inaction*) or a button-press (*HC-action*), in either experiment. In contrast, the Tb component was attenuated in the *FC* condition relative to the *HC-inaction* condition in both experiments. Consistent with the results of Chapter 2, the results of the Tb analyses suggest that the Tb component may index the increased 'sense of agency' associated with the 100% action-effect contingency in the *FC* condition. The P2 component was attenuated in the *FC* condition

relative to both the *HC-inaction* and *HC-action* conditions, in both experiments. The results of the P2 component analyses suggest that effect of *contingency* on neurophysiological indices of sensory attenuation may be indexed by the P2 component.

In both experiments, we found no difference in N1 amplitude between the *FC* condition and *HC* condition, whether triggered by inaction (*HC-inaction*) or a button-press (*HC-action*). Considering the results of Chapter 2 this is perhaps not surprising, as we found that N1 suppression (i.e., relative to a passive condition) did not occur when the motor action was not time-locked to the sound. However, one might nevertheless have expected differences in N1 amplitude between the *FC* and *HC* conditions, considering the different probabilities under which sounds occurred. Under the predictive coding account of perception, neuronal responses to stimuli have been argued to reflect prediction errors (Friston, 2005). In accordance with this account, stimuli that are more predictable trigger smaller neuronal responses than unpredictable stimuli because they result in smaller prediction errors (Schafer et al., 1981; Bendixen, SanMiguel, & Schröger, 2012; SanMiguel et al., 2013; Timm et al., 2013). Related to this, Roth et al. (1976) investigated the effects of probability on auditory processing by delivering auditory stimuli in which a sequence of regularly occurring 65 dB pip sounds were randomly interrupted by white noise bursts. Half of the white noise bursts were preceded by a warning tone (and were thus highly predictable) and half were not (and were thus not predictable). They found that passively presented unpredictable white noise bursts elicited larger N1 amplitudes than passively presented predictable noise bursts. Given the results of Roth et al., (1976), one might expect that the N1 amplitude generated in the *HC* conditions would be larger than in the *FC* condition, considering that the occurrence of the sounds was less predictable in the *HC* conditions. One potential explanation for this result may be the fact that our design required presenting twice as many *HC* blocks as *FC* blocks in order to equalize the number of trials in which the sound

was presented. Since it has been shown that neural responses to repetitive stimuli become smaller over time (Hsu, Hämäläinen, & Waszak, 2014), it is possible that the neural response to the repetitive stimuli in the *HC* conditions decreased over time, which would counteract any ‘N1-enhancing’ effect of stimulus unpredictability in these conditions.

The Tb component was suppressed in the *FC* condition only when compared to sounds in the *HC-inaction* condition. The fact that this reduction in Tb occurred when sounds in the *HC* condition were triggered by inaction, regardless of whether sounds in the *FC* condition were triggered by a willed inaction (Experiment 3) or a button-press (Experiment 4), makes the role of the motor action unclear in terms of its effect on Tb amplitude. In Chapter 2, it was noted that the experimental structure might cause participants to engage in *judgements of agency*, rather than the *feeling of agency* that might be better reflected in the traditional self-stimulation task (Schafer & Marcus, 1973). We previously suggested that the Tb component may index differences in the judgement of agency. The idea that the Tb component may index the judgement of agency is consistent with the results of the present chapter. In the *FC* condition, participants would be expected to judge themselves as having high agency, given that every one of their actions (or inactions) led to a sound 100% of the time. On the other hand, participant judgements of agency would be expected to be lower in the *HC* conditions (i.e., “my button press only sometimes causes the sound”). This pattern of results is consistent with those of Chapter 2, where participants who had high levels of agency demonstrated Tb suppression compared to conditions where they did not have agency. This interpretation could be strengthened by also asking participants the level of control they felt they experienced over sounds across conditions.

However, when considering the contrasts in Tb amplitude between the *FC* condition and the two *HC* conditions, the only significant difference was between the *FC* condition and the *HC-inaction* condition. This was true whether sounds in the *FC* condition were triggered

by action or inactions. A potential explanation for this is that participants judged themselves to have partial agency over sounds generated during the *HC-action* condition. Even though in actual fact the probability of a tone resulting from a button-press was only 50%, the existence of the button-press meant that a tenuous connection could be made between the action and effect (similarly to the phenomenon of ‘illusory control’ (Dixon, 2000; Harris & Osman, 2012). Given that the previous pattern of results in Chapter 2 show that increased judgements of agency lead to suppressed Tb amplitude, it may be the difference in agency attribution that led to the observed discrepancies (although discrepancy might be an overstatement) between the *HC-action* and *HC-inaction* conditions.

Across both experiments, the P2 component was suppressed in the *FC* condition relative to both *HC* conditions (i.e., *HC-inaction* and *HC-action*). The functional significance of the P2 component is less clear than that of the N1 component (Crowley & Colrain, 2004). For example, although the P2 component has shown results like that of the N1 component in previous studies of sensory attenuation (that is, suppression of the *active* condition relative to the *passive* condition (Knolle et al., 2012; Horváth & Burgyán, 2013)), it has also demonstrated opposite results (Pinheiro et al., 2019), although the P2 enhancement (that is, enhancement of the *active* condition relative to the *passive* condition) was only present when there was a delay between the button-press and the resulting sound. These inconsistent results may be attributed to the fact that factors underlying N1 and P2 suppression are likely caused by different factors (Knolle et al., 2012; van Elk et al., 2014), even though they have traditionally been seen as part of a single ‘N1-P2’ complex (Crowley & Colrain, 2004)

The experiments of Chapter 2, which used essentially the same experimental paradigm, demonstrated P2 enhancement – rather than suppression – in the *active* condition relative to the *passive* condition. In the current chapter we observed P2 suppression; it is unclear to us what factors are contributing to this suppression, and why the P2 results for this

chapter differed from the results of Chapter 2. Roth et al. (1976) demonstrated that sounds with a higher probability elicited N1 components with smaller amplitudes but P2 components with larger amplitudes. The results in this chapter contradict this; sounds that were presented in the *FC* condition (and hence had a 100% probability of occurring after a button-press) instead showed smaller P2 amplitudes compared to lower-probability sounds in the *HC* condition. More research is needed to elucidate the nature of the relationship between stimulus probability and P2 amplitude. One possibility is that the P2 component has been associated with attention and categorization processes (García-Larrea et al., 1992; Crowley & Colrain, 2004, Lijffijt et al., 2009). A review by Crowley and Colrain (2004) noted that an *increase* in the attentiveness of the participant resulted in a *decrease* in the amplitude of the P2 component, and vice versa. Considering that the *HC* conditions spanned twice the amount of time compared to the *FC* condition, it is possible that participants' attention may have dropped over the course of the experiment, resulting in an increase in the amplitude of the P2 condition in the *HC* conditions relative to the *FC* condition.

One limitation of the current series of experiments was that – due to lack of time in the experimental session – we were not able to include a *passive* condition, as is common in both the traditional self-stimulation paradigm, and as we included in the modified paradigm we introduced in Chapter 2. As a result of this, we are unable to make a direct comparison to the results of that in the previous chapter and were thus unable to determine the effect of manipulating action-outcome contingency on the phenomenon of sensory attenuation. We aim to address this question in the next experimental chapter. In the future, it would be worthwhile conducting similar experiments with a between-subjects design, with one group completing a *FC* condition contrasting with a *passive* condition, and another group completing the *HC* conditions contrasting with a *passive* condition.

In conclusion, the results of the study suggest that differences in action-effect contingency may be indexed by the P2 and Tb components rather than the N1 component. As previously discussed in Chapter 2, the results are consistent with the idea that the Tb component may indexes judgements of agency, with participants in the *FC* condition experiencing full agency over the sounds as opposed to partial agency in the *HC* conditions. The results of the N1 analyses provide further support for the idea that N1 amplitude is not modulated by actions (or willed inactions) that are not time-locked to sounds.

A central design feature of the current paradigm is that the ‘action’ (i.e., either a button-press, or a willed inaction) was temporally dissociated from the ‘outcome’ (i.e., the sound). While this design feature allowed us to explore the neurophysiological index of ‘sense of agency’ while minimizing the potential confounds of motor-evoked activity, it is – we suggest – likely responsible for our failure to identify any modulation of the N1 component in the experiments presented in Chapters 2 and 3. Given this, we suggest that it would be worthwhile studying the role of contingency in a more traditional self-stimulation paradigm in which the ‘action’ is time-locked to the ‘outcome’, and for which we would expect to observe N1-suppression in the *active* condition relative to the *passive* condition, based on the existing literature. This is the primary aim of the next, and final, experimental chapter.

Chapter 4: Investigating the role of action-outcome contingency in the ‘traditional’ sensory attenuation paradigm

4. 1. Preamble

The results of Chapter 3 provided evidence that the P2 component may index differences in action-outcome contingency in the case where sounds are not time-locked to button-presses. Furthermore, they also provided evidence that the Tb component may index *judgements of agency*, which also corroborates the results of Chapter 2. However, the fact the sounds were not time-locked to the motor actions (or willed inactions) may be responsible for why we did not observe any evidence of N1 suppression (in Chapter 2), or any evidence that N1 amplitude is modulated by differences in contingency (in Chapter 3). In the present chapter, we investigated the role of action-outcome contingency in the context of a more ‘traditional’ self-stimulation paradigm. We did this for two reasons. Firstly, due to the Covid-19 pandemic in 2020 and 2021, all face-to-face data collection was suspended. Therefore, the experiment of this chapter is based on data previously collected for an undergraduate student project. Coincidentally, the undergraduate project also investigated the role of contingency in sensory attenuation but used the traditional self-stimulation paradigm. Secondly, we thought it would be worthwhile investigating the role of contingency on the sensory attenuation effect using the ‘traditional’ self-stimulation paradigm, on which most of the existing sensory attenuation literature is based. In Chapter 3, the effect of variations in action-outcome contingency was only observed in the Tb component, which we linked to between-condition differences in judgements of agency. The aim of the present chapter was to investigate the role of contingency on N1-suppression, which we hypothesize will only occur in the case where sounds are time-locked to willed actions, such as occurs in the ‘traditional’ self-stimulation design.

4. 2. Abstract

Our neurophysiological response to self-generated stimuli is suppressed compared to physically identical stimuli that is externally generated. Dubbed sensory attenuation, this well-studied phenomenon has mostly been investigated by comparing ERPs evoked by self-initiated and externally generated sounds. However, most studies have assumed a uniform action-effect contingency, in which a motor action leads to a resulting sound 100% of the time. In this experiment Chapter, we investigated the effect of manipulating the probability of action-effect contingencies (*Contingency*) on the traditional self-stimulation paradigm (*Production*), where self-initiated sounds which are time-locked to button-presses are compared to externally generated sounds. Participants observed a fixation cross while pressing a button to generate a sound (*active*), during which EEG was recorded. The probability of the sound occurring was either 100% (*active 100*) or 50% (*active 50*). Participants also passively listened (*passive*) to the same sounds so that probabilities were either 100% (*passive 100*) or 50% (*passive 50*). The results of the experiment suggest that the N1 component is mediated by *Production* and *Contingency*. Furthermore, Tb amplitude was modulated by *Contingency* but not *Production*, suggesting that the Tb component is modulated by higher level forms of prediction such as *judgements of agency* but not *feelings of agency*. These results help to corroborate the earlier results of the previous Empirical Chapters.

4. 3. Introduction

Sensations arising from self-generated movements evoke smaller neurophysiological responses than externally generated sensations, even when the evoking stimuli are physically identical. This phenomenon is known as sensory attenuation (Hughes, Desantis, & Waszak, 2013). The neurophysiological aspect of sensory attenuation has been most commonly investigated in the auditory domain, by using EEG/MEG to compare the evoked response to self-initiated and externally initiated sounds (Schafer & Marcus, 1973; Martikainen, Kaneko, & Hari, 2005; Aliu, Houde, & Nagarajan, 2008; Baess et al., 2009; Ford, Roach, & Mathalon, 2010; Gentsch & Schütz-Bosbach, 2011; Horváth, 2015; Pinheiro et al., 2019, 2020). A large body of literature shows that certain components of the auditory-evoked potential are reduced in amplitude when participants hear sounds initiated by their own motor actions (e.g., overt speech, button-press elicited tones), compared to when they passively listen to the same sounds. This effect has been most commonly observed with the N1 component (Bäß, Jacobsen, & Schröger, 2008; Elijah, Pelley, & Whitford, 2018; Mifsud et al., 2016; Neszmélyi & Horváth, 2017; Oestreich et al., 2016; van Elk et al., 2014; Klaffehn et al., 2019; Pinheiro et al., 2019), but has also been identified with the Tb (SanMiguel et al., 2013; Saupe et al., 2013) and P2 components (Knolle et al., 2012; Horváth & Burgyán, 2013).

While there are now a large number of studies that have investigated the phenomenon of sensory attenuation, there are still notable gaps in the literature (Hughes, Desantis, & Waszak, 2013; Horváth, 2015). One question that has been sparsely investigated concerns the role of contingency in sensory attenuation (Horváth, 2015). Here, we define contingency as *the probability of a specific sensory outcome (e.g., a sound) arising as a result of a specific willed action (e.g., a button-press)*.

Self-stimulation experiments have typically had action-effect contingencies of 100%, meaning that the action (e.g., the button-press) produces a sound in 100% of trials (Horváth,

2015). Action-effect contingencies— in ecological settings— do not always occur in such a uniform manner as they have traditionally been done in the laboratory setting. People sometimes incorrectly predict the outcome of an action (for example, when trying to guess the outcome of a button-press on a slots machine). It stands to reason that our neurological apparatus must be equipped to deal with variabilities in action-effect contingencies in ecological settings. Therefore, as argued by Horváth (2015), the effect of contingency is an important gap in the sensory attenuation literature that ought to be examined.

The aim of the present chapter is to thus to investigate the role of contingency in the sensory attenuation phenomenon. In contrast to the ‘novel’ paradigm used in Chapters 2 and 3, the current chapter used a more ‘traditional’ self-stimulation paradigm in which the sounds were time-locked to button presses. As discussed previously, a limitation associated with the traditional self-stimulation paradigm is that the motor action, *per se*, elicits activity in the EEG which can become confounded with the auditory-evoked potential in the ‘active’ (self-generated) condition. Thus, in order to compensate for potential motor-evoked potentials, the current study implemented a third condition (i.e., in addition to the two *active* and *passive* conditions) called the *motor* condition. The *motor* condition is commonly used in self-stimulation studies of this nature (Neszmélyi & Horváth, 2017; Neszmélyi & Horváth, 2019; Horváth, Bíró, & Neszmélyi, 2018). In the *motor* condition, participants are required to press a button, however no sound is delivered following the button press. The ERP elicited by the *motor* condition is subtracted from the *active* condition ERP, ostensibly creating an ERP that is ‘corrected’ from the confounding effects of motor-evoked potentials. This ‘motor-corrected-active’ condition can then be compared to the *passive* condition ERP, and a difference between these waveforms is taken as evidence of ‘sensory attenuation’.

As previously discussed, we did not find evidence of N1-suppression in Chapters 2 and 3. Rather, the locus of suppression was found in the Tb component - which we argued

was an index of participants' sense of agency over the sound - and the P2 component. We argued that a reason we did not observe N1-suppression in Chapters 2 and 3 was that the motor action was not time-locked to the sound in these experiments. Previous studies which have identified N1 suppression in the context of sensory attenuation (Schafer & Marcus, 1973; Bäß, Jacobsen, & Schröger, 2008; Knolle et al., 2012; Horváth & Burgyán, 2013; SanMiguel, Todd, & Schröger, 2013; Saupe et al., 2013; Elijah, Pelley, & Whitford, 2018; Neszmélyi & Horváth, 2017; Oestreich et al., 2016) have all used experiments resembling that of the 'traditional' self-stimulation experiment in which the motor action (typically a button-press) is time-locked to the sound. Therefore, we first hypothesised that N1 suppression would be observed in the present study, with the N1 component in the *active* condition being smaller than the N1 component in the *passive* condition. Secondly, if N1 suppression is influenced by differences in action-outcome contingencies (i.e., the probability of the sound following the button-press), we further hypothesised that the N1 suppression effect would be larger in the *100* condition (when the probability of a sound occurring after a button-press is 100%) than the *50* condition (when the probability of a sound occurring after a button-press is 50%), as self-generated sounds in the *100* condition are more predictable.

4. 4. Method

4. 4. 1. Participants

Forty-nine undergraduate students from the University of New South Wales (Sydney, Australia) participated in the study in exchange for course credit ($n = 49$). All participants gave written informed consent prior to the experiment. Two participants were removed from analysis due to insufficient number of artifact-free epochs (as described in EEG Recording and Analysis) leaving a final sample of $n = 47$ participants (mean age = 20.53 years, SD =

5.04, 18 females). The study was approved by the Human Research Ethics Advisory Panel (Psychology) at the University of New South Wales.

This experiment was originally planned to be run using the same visual stimuli described in the preceding empirical chapters (Chapters 2 and 3) but modified to facilitate the implementation of the ‘traditional’ self-stimulation design. Due to the COVID-19 pandemic, however, face-to-face data collection was suspended for the majority of 2020 and 2021. As a result, the experiment described in this chapter is based on data previously collected for an undergraduate student project in the laboratory of Prof. Thomas Whitford. The current data also looks at the question of contingency but in the classical self-stimulation paradigm (Schafer & Marcus, 1973). An unfortunate consequence of not being able to use the experimental stimuli developed in Chapters 2 and 3 is that we were not able to control for the confounding effects of temporal predictability and temporal control (Hughes et al., 2013).

4. 4. 2. Stimuli, Materials, and Procedure

The audio stimulus was a sinusoid tone of frequency 1000 Hz, 100 ms duration, with a 5 ms linear rise/fall time. Audio stimuli were sent to participants through Sennheiser HD 210 headphones. Audio input/output was controlled by a specially written MATLAB script and was delivered via an AudioFile Stimulus Processor (Cambridge Research Systems). Participants made responses by pressing the space bar of a low-latency keyboard (DuckyShine 4, 1000 Hz report rate). Visual stimuli were displayed on a 24-inch, BenQ XL2420T monitor.

The experiment investigated the effects of *Production* (the difference between the *active-corrected* (that is, *active* minus *motor*) and *passive* conditions) and *Contingency* (the difference between sounds that were generated with a 100% probability of occurring and sounds that were generated with a 50% probability of occurring) on sensory attenuation.

There were six conditions in the experiment: the *active 100*, *motor 100*, *active 50*, *motor 50*, *passive 100*, and *passive 50* conditions. A schematic of the conditions and the order in which the conditions appeared is presented in Figure 1. During each condition, participants observed a fixation cross in the middle of the screen, which remained for the duration of the block. A fixation cross design is sub-optimal when considering factors such as temporal predictability, as the temporal onset of sounds is more predictable in the *active* conditions compared to the *passive* conditions. However, the COVID-19 pandemic prevented us from collecting new data, thus forcing us to use old data collected using a slightly sub-optimal design (compared with the better controlled designs used in the previous empirical chapters).

In the *active 100* condition, participants pressed a button at regular intervals (at least two seconds apart) whenever they felt the urge. A tone was always presented following the button-press, with a near zero latency between button-press and tone (< 5 ms). In the *motor 100* condition, participants performed the same actions as they did in the *active 100* condition, except that no sound was played following the button-press. The *active 50* and *motor 50* conditions co-occurred within the same block. Again, participants performed the same actions as they did in the *active 100* and *motor 100* conditions. However, sounds would only play on a random 50% of trials (*active 50*). On 50% of the trials, no sound was played following a button-press (*motor 50*). In the *passive 100* and *passive 50* conditions, participants were instructed to passively listen to sounds throughout the block. The sounds played in the *passive 100* and *passive 50* blocks were recordings of same series of sounds that participants generated in the *active 100* and *active 50* blocks respectively. This was done to ensure that the inter-stimulus intervals (ISI) were consistent across conditions, as ISI has been shown to influence the amplitude of the N1 components (Röder, Rösler, & Neville, 1999; Pereira et al., 2014).

The experiment consisted of 14 blocks in total. Each block contained 40 trials. There were two blocks each of the *active 100*, *passive 100*, and *motor 100* conditions, and four blocks each of the combined *active 50/motor 50* conditions and *passive 50* conditions. There were twice the number of 50 blocks compared to 100 blocks to achieve equal epoch numbers for the statistical analysis (as sounds only occurred on 50% of trials in the 50 blocks). The order of blocks was counterbalanced, with the exception that the *active* conditions always preceded the *passive* conditions to allow the ISIs generated in the *active* conditions were used in the *passive* conditions.

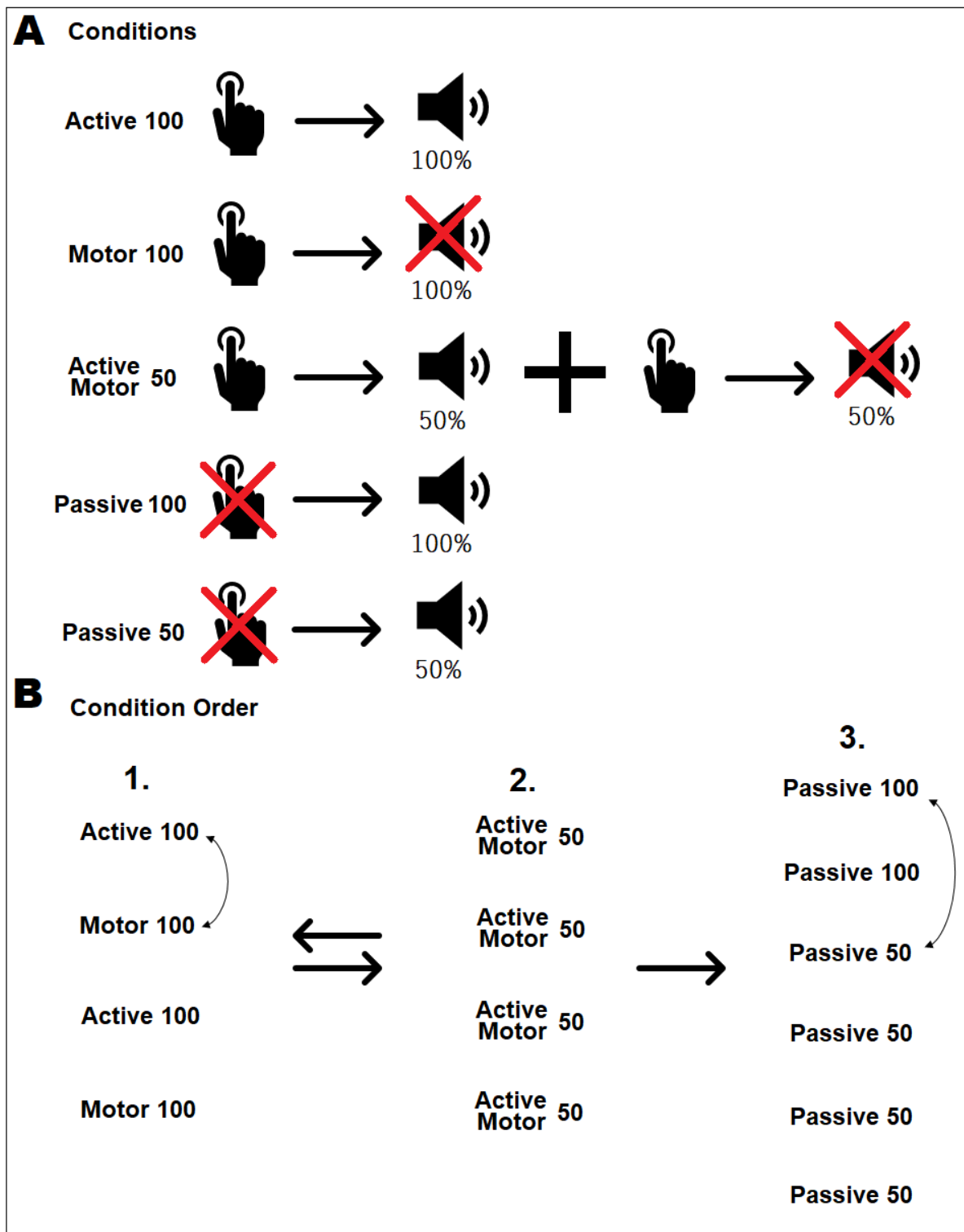


Figure 4. 1. Experiment schematic (A) Conditions of the experiment: In the *active 100* condition, participants pressed a button at regular intervals whenever they felt the urge. Sounds always followed button-presses in this condition. In the *motor 100* condition, participants pressed the button whenever they felt the urge, but no sound was played following the button-press. The *active 50* and *motor 50* conditions co-occurred within the

same block. Again, participants performed the same actions as they did in the *active 100* and *motor 100* conditions (i.e., pressed a button whenever they felt the urge). However, sounds would only play on 50% of the trials (*active 50* trials). On 50% of the trials, no sound would be played following a button-press (*motor 50* trials). In the *passive 100* and *passive 50* conditions, participants were instructed to passively listen to sounds throughout the block. (B) Order of the conditions: Participants completed either part 1 (*active* and *motor 100*) or part 2 (*active/motor 50*), the order of which were counterbalanced. In part 1, the first instance of *active 100* and *motor 100* were counterbalanced. Part 3 (the *passive* conditions) was completed last, as the conditions were a replay of the sounds produced during the active conditions. The first instance of *passive 100* and *passive 50* were counterbalanced.

4. 4. 3. EEG Recording and Analysis

EEG was recorded with a BioSemi ActiveTwo system from 64 Ag/AgCl active electrodes (*P1, FPz, FP2, AF7, AF3, AFz, AF4, AF8, F7, F5,F3, F1, Fz, F2, F4, F6, F8, FT7, FC5, FC3, FC1, FCz, FC2, FC4, FC6, FT8,T7, C5, C3, C1, Cz, C2, C4, C6, T8, TP7, CP5, CP3, CP1, CPz, CP2, CP4,CP6, TP8, P9, P7, P5, P3, P1, Pz, P2, P4, P6, P8, P10, PO7, PO3, POz,PO4, PO8, O1, Oz, O2, Iz*). A vertical electrooculogram (EOG) was recorded by placing an electrode above and below the left eye; a horizontal EOG was recorded by placing an electrode on the outer canthus of each eye. Electrodes were also placed on each mastoid, and the nose. During data acquisition, the reference was composed of sites CMS and DRL, and the sampling rate was 2,048 Hz.

For data analyses, we re-referenced the EEG data offline to the nose electrode, as is common in studies investigating the components-of-interest, and necessary for extracting the Tb component (Näätänen & Picton, 1987; SanMiguel et al., 2013; Woods, 1995). Data were notch filtered (50Hz) to remove mains artefact and band-pass filtered from 0.1 to 30 Hz using a phase-shift-free Butterworth filter. The filtered data were segmented into 500 ms epochs, from -100 ms pre-stimulus to 400 ms post-stimulus. Only trials in which the auditory stimulus were played were analyzed. Epochs were baseline-corrected to the mean voltage from -100 to 0 ms. We corrected the epochs for eye blinks and movement artefacts using the

technique described in Gratton, Coles, and Donchin (1983) and Miller, Gratton, and Yee (1988). We excluded all epochs with signals exceeding peak-to-peak amplitudes of 200 uV and had a maximal allowed voltage step of 50 uV/ms. We analysed the amplitudes of the N1, Tb and P2 components of the auditory-evoked potential. These amplitudes were calculated as the average voltage within time-windows (30 ms width). The centers of the time-windows were defined by first calculating difference waves between corresponding *active-corrected* and *passive* waveforms, averaging the two difference waves together, then using the collapsed localiser approach to identify the components-of-interest (Luck & Gaspelin, 2017). The collapsed localiser approach is a technique whereby one first averages (or ‘collapses’) the ERP waveforms across all conditions for all participants. The components-of-interest (e.g., N1, Tb, P2) are identified on this ‘collapsed’ waveform, and a time-window is centred around these peaks, which is then used for the statistical analysis of the original (or ‘uncollapsed’) waveforms (Luck & Gaspelin, 2017).

For the N1, Tb, and P2 components, mean voltage in the analysis window was submitted to a 2 (Production: *active-corrected*, *passive*) x 2 (Contingency: *100*, *50*) repeated-measures ANOVA. Electrodes of interest were the Fz, FCz, and Cz electrodes for the N1 component, T7 and T8 for the Tb component, and FCz, Cz, and CPz for the P2 component. For the N1 and P2 components, these electrodes were chosen to be consistent the previous chapters, and also because these were the electrodes at which the components were maximal on the collapsed localizer waveform. Electrodes for the Tb component (T7 and T8) were based on recommendations by Tonnquist-Uhlen et al. (2013) and SanMiguel et al. (2013) and were also consistent with the previous chapters. Although the electrode selection for the N1 and P2 components would have benefited from being identical to that of Chapter 2, as that would have allowed for a more direct comparison of the results, this was not possible because

the manuscript reviewer for Chapter 2 had asked for the electrode selection for the N1 and P2 components to be expanded.

4. 4. 4. Results

There was an average of 76.4 (SD = 11.6) usable epochs in the *active 100* condition, 73.6 (SD = 10.6) in the *active 50* condition, 75 (SD = 16.9) in the *passive 100* condition, and 73.8 (SD = 10.2) in the *passive 50* condition. There was a maximum number of 80 epochs for each of the conditions.

N1

Figure 2 shows the N1 component analysis elicited in the *active-corrected* (i.e., *active* minus *motor*) and *passive* conditions. The N1 component showed the expected fronto-central topography. The time-window for the N1 analysis was centred at 124 ms (based on the N1 peak in the collapsed localizer) and extended from 109 – 139 ms. The repeated measures ANOVA yielded a significant main effect of *Production*, $F(1, 46) = 5.03, p = .030, \eta_p^2 = 0.10$ and a significant main effect of *Contingency*, $F(1, 46) = 20.02, p < .001, \eta_p^2 = 0.30$. The *Production*Contingency* interaction was not significant, $F(1, 46) = 0.26, p = .612, \eta_p^2 = 0.01$. The results indicate that the N1 amplitude of the *active-corrected* condition was smaller relative to the *passive* condition, and that the N1 amplitude was smaller when contingency was 100% compared to when contingency was 50%.

N1

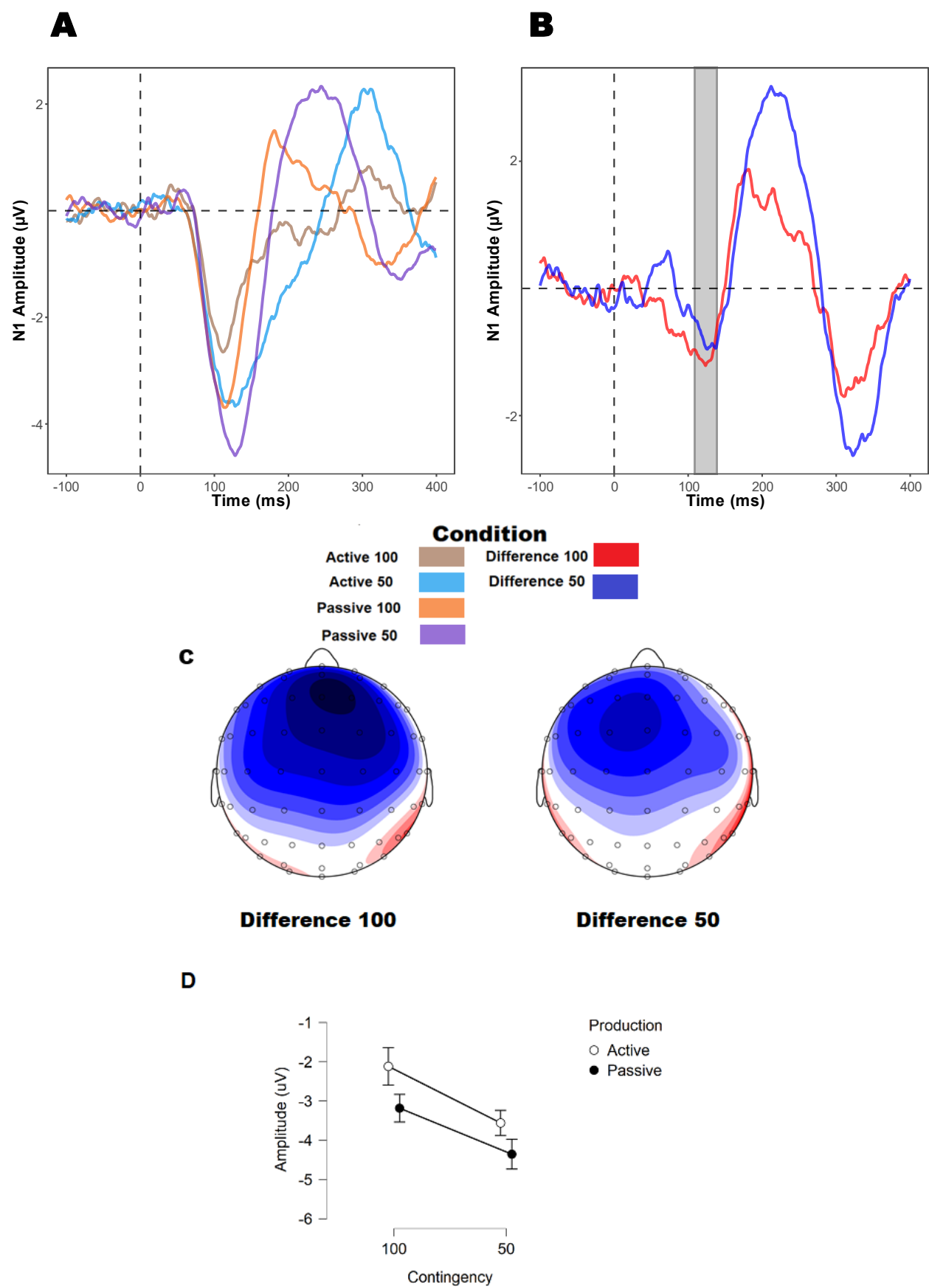


Figure 4. 2. Experiment 5 N1 results (A) Waveforms showing N1 ERPs (at electrodes Fz, FCz, and Cz) elicited by the *active-corrected 100*, *active-corrected 50*, *passive 100*, and *passive 50* conditions. (B) Difference waves contrasting the *100* and *50 conditions* as well as the time window for analysis (109 – 139 ms). *Difference 100* constitutes the difference between *active 100 – passive 100* and *Difference 50* constitutes the difference between *active 50 – passive 50*. (C) Topographic maps of N1 suppression (i.e., active-corrected minus passive) conditions in the *100* (left) and *50* (right) *conditions*. (D) Descriptive plot showing mean N1 amplitude of *active* and *passive* conditions across *Contingency* levels and error bars representing the standard error of the mean.

Tb

Figure 3 (below) shows the Tb component analysis elicited in the *active-corrected* and *passive* conditions. The Tb showed the expected temporal lobe topography. The time-window for the Tb analysis was centred at 152.8 ms and extended from 137.8 – 167.8 ms. The repeated measures ANOVA yielded a significant main effect of *Contingency*, $F(1, 46) = 7.99$, $p = .007$, $\eta_p^2 = 0.15$. The main effect of *Production* failed to reach significance, $F(1, 46) = 0.30$, $p = .588$, $\eta_p^2 = 0.01$. The interaction *Production*Contingency* also failed to reach significance, $F(1, 46) = 0.47$, $p = .494$, $\eta_p^2 = 0.01$. The results suggest that Tb amplitude was smaller when the action-outcome contingency was 100% (i.e., a button-press caused a tone to be played 100% of the time) compared to when it was 50%.

Tb

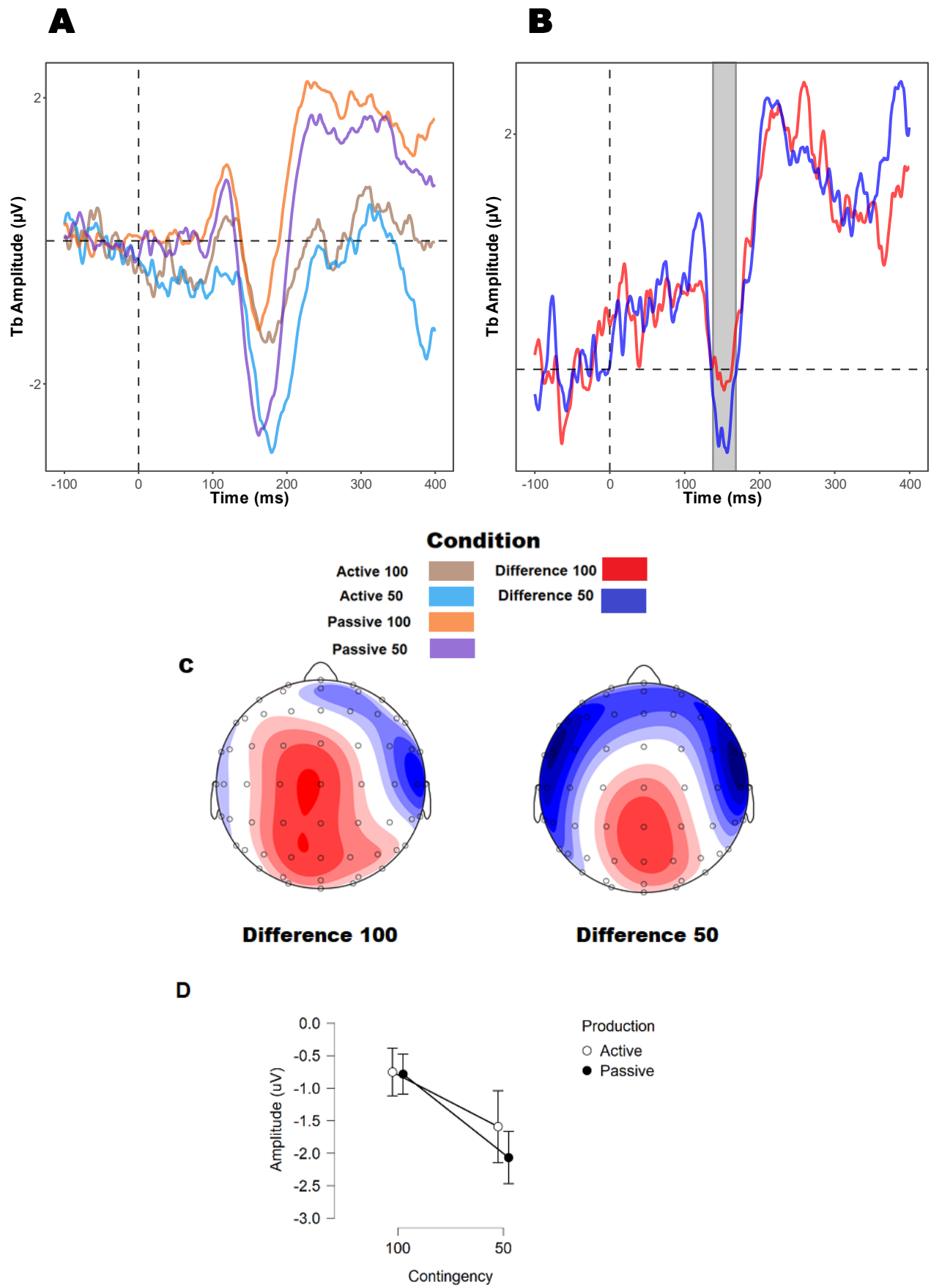


Figure 4. 3. Experiment 5 Tb results (A) Waveforms showing Tb ERPs (at electrodes T7 and T8) elicited by the *active 100*, *active 50*, *passive 100*, and *passive 50* conditions. (B) Difference waves contrasting the *100* and *50* conditions as well as time window for analysis (109 – 139 ms). *Difference 100* constitutes the difference between *active 100* – *passive 100* and *Difference 50* constitutes the difference between *active 50* – *passive 50*. (C) Topographic maps of Tb suppression between *active* and *passive* conditions in the *100* (left) and *50* (right) conditions. (D) Descriptive plot showing mean amplitude of *active* and *passive* conditions across contingency levels and error bars

P2

Figure 4 (below) shows the P2 component analysis elicited in the *active-corrected* and *passive* conditions. It is notable that the P2 component showed a substantially different latency depending on the *Production* condition. The time-window for the P2 analysis was centred at 213.4 and extended from 198.4 – 228.4 ms and based on waveforms that were collapsed across *Production* conditions. The repeated measures ANOVA yielded a significant main effect of *Production*, $F(1, 46) = 53.05, p < .001, \eta_p^2 = 0.54$, as well as a significant *Production*Contingency* interaction, $F(1, 46) = 6.90, p = .012, \eta_p^2 = 0.13$. The main effect of *Contingency* failed to reach significance, $F(1, 46) = 0.03, p = .875, \eta_p^2 < 0.00$. The results suggest that the P2 amplitude of the *active-corrected* condition was smaller relative to the amplitude in the *passive* condition. The significant interaction suggests that an effect of *Contingency* was dependent on *Production* type- that is, sounds that had an 100% probability of occurring elicited P2 amplitudes smaller than sounds that had a 50% probability of occurring, but only in the *passive* condition. A follow-up paired samples t-test found a significant contrast comparing *passive 100* to *passive 50*, $t(46) = -3.40, p = .001, d = -0.30$, confirming that *Contingency* had an effect in the *passive* condition.

P2

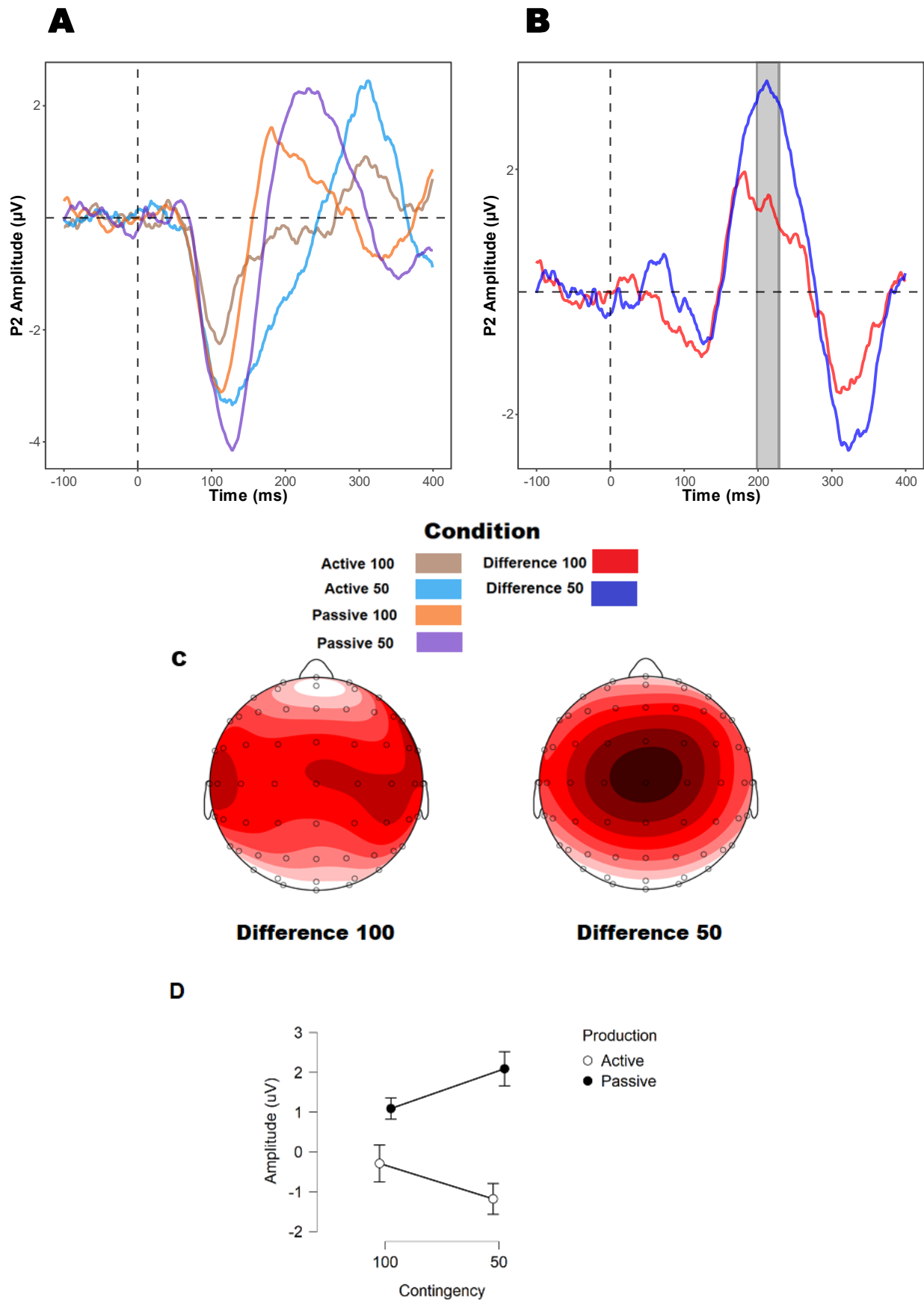


Figure 4. 4. Experiment 5 P2 results (A) Waveforms showing P2 ERPs (at electrodes FCz, Cz, and CPz) elicited by the *active 100*, *active 50*, *passive 100*, and *passive 50* conditions. (B) Difference waves contrasting the *100* and *50* conditions as well as the time window for analysis (198.4 – 228.4 ms). *Difference 100* constitutes the difference between *active 100* – *passive 100* and *Difference 50* constitutes the difference between *active 50* – *passive 50*. (C) Topographic maps of P2 suppression between *active* and *passive* conditions in the *100* (left) and *50* (right) conditions. (D) Descriptive plot showing mean amplitude of *active* and *passive* conditions across contingency levels and error bars

4. 5. Discussion

In the current experiment, we set out to investigate sensory attenuation (operationalized as action-based suppression of the N1, Tb, and P2 components of the auditory-evoked potential) when the contingency between the button-press and sound was manipulated. In contrast to the previous chapters, the present study used a ‘classical’ self-stimulation paradigm in which the motor-action (button-press) was time-locked to the evoked stimulus (tone) (Schafer & Marcus, 1973; Bäß, Jacobsen, & Schröger, 2008; Knolle et al., 2012; Horváth & Burgyán, 2013; SanMiguel, Todd, & Schröger, 2013; Saupe et al., 2013; Elijah, Pelley, & Whitford, 2018; Neszmeélyi & Horváth, 2017; Oestreich et al., 2016)

To summarize the key results:

- The amplitude of the N1 component was suppressed in the *active-corrected* condition relative to the amplitude of the N1 component in the *passive* condition, replicating the results of most of the self-stimulation literature (Bäß, Jacobsen, & Schröger, 2008; Elijah, Pelley, & Whitford, 2018; Mifsud et al., 2016; Neszmeélyi & Horváth, 2017; Oestreich et al., 2016; van Elk et al., 2014; Klaffehn et al., 2019; Pinheiro et al., 2019). Furthermore, the amplitude of the N1 component was also smaller when the contingency between the button-press and the tone was set at 100% (i.e., the button-press always caused a tone to be played) compared to when contingency was set at 50% (i.e., the button-press caused a tone to be played only 50% of the time).

- The amplitude of the Tb component was smaller when the contingency between the button-press and the tone was 100% compared to when the contingency was set at 50%. There were no differences in Tb amplitude between the *active* and *passive* conditions. In other words, there was a main effect of *Contingency* but no main effect of *Production*. Furthermore, there was no significant interaction (*Production*Contingency*).
- The amplitude of the P2 component was suppressed in the *active-corrected* condition relative to the *passive* condition. *Contingency* effects were also detected in the *passive* condition (only); specifically, when contingency was set at 100%, this resulted in smaller P2 amplitudes than when *Contingency* was set at 50%. As discussed further below, complicating the interpretation of this finding is the fact that the P2 scalp distributions were dissimilar between the *100* and *50* conditions, and P2 latency differences were observed between the *active* and *passive* P2 peaks, with the *active* conditions ostensibly not indicating a clear P2 peak.

In the current experiment, we found that both *Production* and *Contingency* mediated N1 amplitude. In contrast with the results of the previous chapters, we found suppressed N1 amplitude in the *active* condition, relative to the *passive* condition, which was consistent with the majority of previous studies in the sensory attenuation literature (e.g., Bäß, Jacobsen, & Schröger, 2008; Elijah, Pelley, & Whitford, 2018; Mifsud et al., 2016; Neszemélyi & Horváth, 2017; Oestreich et al., 2016; van Elk et al., 2014; Klaffehn et al., 2019; Pinheiro et al., 2019). The contrast with previous chapters can be explained by the fact that the current experiment was designed such that sounds were time-locked to the motor action. Previous sensory attenuation studies that have manipulated the delay between action and effect found that delays longer than a few hundred milliseconds abolished the N1 suppression effect (Whitford et al., 2011; Oestreich et al., 2016; Pinheiro et al., 2019), suggesting that N1 suppression is

dependent on the motor action occurring either simultaneously with, or close-in-time to, the resulting sound. The N1 suppression observed here can be explained through the action of corollary discharge-related mechanisms that are explicated by the Internal Forward Model (IFM). As discussed previously in Chapter 1, the mechanistic basis of the IFM is that the brain uses a copy of the outgoing motor command (‘efference copy’) to make predictions (‘corollary discharges’) about the expected sensory consequences of self-initiated movements (Miall & Wolpert, 1996; Crapse & Sommer, 2008). According to the theory, if the sensory feedback matches the predicted feedback (i.e., in terms of both its physical and temporal properties) then the resulting neurological response to the sensory feedback (in this case, the sound) is suppressed (Crapse & Sommer, 2008; Poulet & Hedwig, 2007).

With regards to N1, the other main effect we observed was the influence of stimulus contingency on N1 amplitude. When contingency was set at 100% - and thus the occurrence of the sound was fully predictable on the basis of the button-press – N1 amplitude was smaller relative to when contingency was set at 50% (i.e., the button-press elicited a sound only 50% of the time) and when collapsed across *active-corrected* and *passive* conditions. A key point here is that the *Contingency* condition manipulated the predictability of the sound, although arguably a higher-level form of prediction than corollary discharges, because participants likely have to explicitly form judgements regarding the probability of a sound occurring on a given trial. The fact that we observed effects of *Contingency* suggests that early neurophysiological responses to sound—represented by the N1 component—is likely affected by higher-level influences such as explicit judgements of probability. This lends support to a predictive coding account of perception (Friston, 2005), which states that lower-level sensory predictions are informed by higher levels ‘priors’ in a cortical hierarchy.

The current experiment yielded the classical N1 suppression effect (Bäß, Jacobsen, & Schröger, 2008; Elijah, Pelley, & Whitford, 2018; Mifsud et al., 2016; Neszmeily & Horváth,

2017; Oestreich et al., 2016; van Elk et al., 2014; Klaffehn et al., 2019; Pinheiro et al., 2019) but did not control for differences in temporal predictability between the *active* and *passive* conditions. Of the studies that investigated the effect of temporal predictability sensory attenuation, most found that the magnitude of the effect was reduced (Weiskrantz, Elliot, & Darlington, 1971; Schafer & Marcus, 1973; Hughes et al., 2013), but not entirely abolished (Lange, 2011; Klaffehn et al., 2019; Harrison et al., 2021), when temporal predictability was controlled for. In the previous chapters in this thesis, between-condition differences in temporal predictability were controlled for by means of the ‘ticker-tape’ feature of the experimental stimulus, as this allowed participants to accurately predict, based on an external cue, exactly when they would hear the sound in the passive conditions. Due to the ongoing Covid-19 situation, we were forced to analyse data from a previous experiment which used a methodology that did not control for temporal predictability. While participants could choose when to generate sounds in the *active* condition, participants in the *passive* condition simply heard a recording of the *active* condition sounds, with no cue indicating when the sounds might appear. The key point is that participants were able to anticipate precisely when the sound will occur in the *active* condition (because they themselves are causing these sounds), while there was no indication of when the sounds would occur in the *passive* condition. Consequently, sounds in the *passive* condition were less temporally predictable than sounds in the *active* condition. As mentioned previously, sounds that are more predictable tend to trigger a smaller neuronal response. A study by Roth et al. (1976) investigating the effect of probability on auditory processing of externally generated sounds found that sounds with low probability elicited larger N1 amplitudes under task relevant conditions. Hence, the N1 suppression effect observed in the current experiment may possibly be caused, at least in part, by between-condition differences in the temporal predictability of the stimuli. We discuss this point in more detail in the limitations section of the General Discussion (Chapter 5).

The amplitude of the Tb component was smaller when contingency was set at 100% as opposed to when contingency was 50%. However, there was no effect of *Production* on Tb amplitude; that is, there was no difference in Tb-amplitude between the *active* and *passive* conditions. The main effect of *Contingency* was consistent with a predictive coding account of Tb suppression (Friston, 2005), given that the tones were less predictable in the 50% contingency condition relative to the 100% contingency condition. Consistent with this idea, there is evidence demonstrating that predictive processes mediate Tb amplitude (SanMiguel et al., 2013; Saupe et al., 2013). One explanation for why we did not observe a main effect of *Production* on Tb amplitude is that Tb suppression—unlike N1 suppression—seemingly does not depend on an action co-occurring with the stimulus, based on the results of the previous chapters. Unlike experiments in the previous empirical chapters, the current experiment included sounds that were time-locked to the action. We suggest that this would have resulted in participants experiencing the *feeling of agency* as opposed to the *judgement of agency* (Synofzik et al., 2008), the role of which we have emphasized in the previous empirical chapters. The *feeling of agency* is simply the sense of agency one experiences when they perform a motor action that is immediately followed by a sensory event. This is what the literature typically refers to when discussing agency within the context of comparator models (Synofzik et al., 2008). The *judgement of agency*, on the other hand, requires an explicit cognitive judgement of one's agency, and may rely less on sensorimotor indicators. As argued in Chapter 2, we suggest that the Tb component is more likely to index *judgements of agency* as opposed to the *feeling of agency*. Likewise, when accounting for differences in stimulus predictability (arising from the experimental manipulations of contingency), participants will likely have to make conscious *judgements* regarding the probabilities of sound onset. Taken together, these factors may explain why effects of *Contingency* were found, while effects of *Production* were not. Furthermore, it should be noted that there

appears to be more signal variability in the -100 ms to 100 ms window for the Tb component. This signal variability may point to issues in data quality or data collection and may help to explain why effects of *Contingency* were not found. Additionally, further research would need to be conducted regarding what processes contribute to the mediation of Tb amplitude. This is because higher-order cognitive processes (such as cognitive judgements) are typically associated with ERP components occurring no earlier than 300 ms.

We observed a main effect of *Production* on the P2 component (i.e., comparing the *active* and *passive* conditions) and a significant interaction between *Production* and *Contingency*. P2 amplitude in the *active* conditions were suppressed relative to P2 amplitudes in the *passive* conditions, when collapsing across *Contingency*. We also find P2 suppression of the *100* condition relative to the *50* condition, but only in the *passive* condition. If we look at the topographic maps of P2-suppression (i.e., *active-corrected* minus *passive*), we can see that the distribution of voltages is dissimilar for between the *100* and *50* contingency conditions. The P2 suppression of the *50* conditions show a positivity at the central electrodes, whereas the *100* condition shows bilateral positives at temporal electrodes. These differences in scalp topography suggest that the underlying processes giving rise to the P2-suppression effect were different for both *Contingency* conditions, most likely due to the differences in the probability of the auditory stimuli.

Furthermore, we also found the latencies of the P2 peak to be dissimilar between the *active* and *passive* conditions, with the *active* condition ostensibly not having a peak in the P2 window, but rather a peak closer to the P3 range (Polich, 2012). However, given that the P2 is an obligatory component of the auditory-evoked ERP (Näätänen & Picton, 1987; Crowley & Colrain, 2004; Wagner, Shafer, Martin, & Steinschneider, 2013), one possible explanation is that the P2 peaks were obscured by other overlapping components, such as the N2 and P3 components. The auditory N2 component, having bilateral sources in auditory cortex

(Bruneau & Gomot, 1998; Čeponienė, Rinne, & Näätänen, 2002), has been implicated in numerous functions, including stimulus discrimination (Ritter, Simson, & Vaughan, 1983; Satterfield, Schell, Nicholas, Satterfield, & Freese, 1990) and orientation response (Loveless, 1983). The P3 component, located in the midline electrodes, is a well-studied component that has been argued to reflect processes related to stimulus discrimination (Polich, 2012) context updating (Donchin et al., 1986; Polich, 2012), and memory encoding (Kok, 2001; Polich, 2012).

The functional significance of the P2 is less clear than the N1, but it has been shown to be related to attention and categorization processes (García-Larrea et al., 1992; Crowley & Colrain, 2004; Lijffijt et al., 2009). Our finding of P2 suppression in the *active* condition relative to the *passive* condition is broadly consistent with previous literature (Knolle et al., 2012; Horváth & Burgián, 2013), although in general the evidence for P2 suppression is more inconsistent when compared to N1 suppression (Pinheiro et al., 2019), which shows a more consistent pattern of N1 amplitude reductions in the *active* condition relative to the *passive* condition (Bäb, Jacobsen, & Schröger, 2008; Elijah, Pelley, & Whitford, 2018; Mifsud et al., 2016; Neszmeilyi & Horváth, 2017; Oestreich et al., 2016; van Elk et al., 2014; Klaffehn et al., 2019; Pinheiro et al., 2019). The fact that we also found P2 amplitude reductions in the *100* condition relative to the *50* condition, but only in the *passive* condition, is perhaps surprising, given that Roth et al. (1976) demonstrated that the P2 amplitude was smaller when evoked by a high-probability sounds. One possible reason for this discrepancy between the *active-corrected* and *passive* conditions may lie with the fact that sounds were generally less predictable in the *passive* condition as there were no visual stimuli to aid in temporal predictability.

Aside from the issue of temporal predictability mentioned earlier, another limitation of the present experiment involved the inclusion of the third *motor* condition. Due to the

COVID-19 pandemic, the data for this experimental chapter was based on a previous undergraduate student project, which did not use the ticker-tape paradigm of the previous two chapters (which we suggest as a good idea for future research and would better control for temporal predictability). The previous project relied instead on the traditional self-stimulation paradigm (Schafer & Marcus, 1973). The third *motor* condition was included to control for motor-evoked potentials associated with the performance of the motor action *per se*.

Subtracting the ERP of the *motor* condition from the ERP of the *active* condition is a well-established technique in sensory attenuation studies, which is aimed at creating an motor-corrected active auditory-evoked potential that is comparable to the auditory-evoked potential elicited in the *passive* condition (Bäß, Jacobsen, & Schröger, 2008; SanMiguel, Todd, & Schröger, 2013; Elijah, Pelley, & Whitford, 2018; Mifsud et al., 2016; Oestreich et al., 2016;. However, several arguments have been made that question the assumptions behind this subtraction (Neszmélyi & Horváth, 2017; Neszmélyi & Horváth, 2019; Horváth, Bíró, & Neszmélyi, 2018). For example, Neszmélyi and Horváth (2017) demonstrated that in trials where participants pressed a button, having a sound follow the motor action served as confirmation that the participants' motor action was performed correctly. In *motor-only* conditions (in which no sound followed the button press and thus the participant had no confirmation that their action had been performed correctly), participants overcompensated by pressing the button harder. The authors therefore argued that the simple subtraction of the *motor* condition did not create a valid motor-corrected auditory-evoked potential that was comparable to the *passive* condition.

In conclusion, the results of the experiment suggest that the N1 component is mediated by *Production* and *Contingency*. In this experiment, *Production* was operationalized as whether sounds were self-generated (*active* condition) or externally generated (*passive* condition). *Contingency* was operationalized as the probability in which

sounds occurred (either 100% or 50% probability). We observed Tb suppression to the manipulation in *Contingency* but not to *Production*, suggesting that the Tb component is modulated by higher level forms of prediction such as *judgements of agency* but not *feelings of agency*, corroborating the results found in Chapter 2. On the other hand, effects of *Production* and *Contingency* were mixed when considering the P2 component, with latency and voltage differences suggesting the need for further research into the relationship between the P2 component and probability within the context of sensory attenuation. When considered alongside the results of the previous chapter, the fact that we observed N1 suppression in the current experiment suggests that for N1 suppression to occur, the sensory stimulus (in this case, the sound) must occur simultaneously with, or close-in-time-to, the eliciting motor action (in this case, the button-press).

Chapter 5: General Discussion

The present thesis set out to explore two previously understudied factors relating to the phenomenon of sensory attenuation: namely, the relation between sensory attenuation and a person's sense of agency (Experiments 1 and 2) and the relationship between sensory attenuation and action-effect contingency (Experiments 3, 4, and 5). In the first four experiments, we used a methodological design adapted from Whitford et al. (2017) and Jack et al. (2019) in which actions were temporally dissociated from sensations. In Experiment 5, we employed a more traditional self-stimulation paradigm (Schafer & Marcus, 1973) like that used by most studies in the sensory attenuation literature. Participant samples across all five experiments were unique. The findings for the three ERP components (N1, Tb, P2) across all experiments are summarised below (Figure 5.1).

In Experiments 1 and 2, we investigated the relation between agency and sensory attenuation by having participants choose— via the performance of either a *willed inaction* (Experiment 1) or a *willed action* (Experiment 2)— whether a sound would be played. In Experiment 1, participants watched a moving, marked tickertape while EEG was recorded. In the *active* condition, participants had to decide whether or not to press the button by a certain point on the tickertape (the 'decision time'). If the participant decided *not* to press the button, then a sound would be subsequently played (exactly one second after the 'decision time'). In contrast, if they decided to press the button, this would inhibit the sound from playing. In the *passive* condition, participants passively watched the tickertape animation, but had no control over whether the sound would be played. At the beginning of each trial, the participant was informed as to whether or not they would hear the sound. Experiment 2 had an identical design as that of Experiment 1, except that the action-effect contingency was reversed; that is, in the *active* condition, it was the button press (rather than the willed inaction) that triggered the subsequent presentation of the sound. The *passive* conditions were identical across both

N1 Component	Experiments 1 & 2	N1 suppression driven by motor processes rather than sense of agency <i>per se</i>
	Experiments 3 & 4	No N1 suppression when motor action not time-locked to sound
	Experiment 5	N1 suppression found when sounds self-generated compared to externally generated sounds N1 amplitude smaller when sounds have 100% compared to 50% probability sounds
Tb Component	Experiments 1 & 2	Tb amplitude smaller in the <i>active</i> condition relative to the <i>passive</i> condition, suggesting that it is a marker for sense of agency
	Experiments 3 & 4	Tb amplitude smaller when sounds have 100% probability compared to 50% probability sounds, suggesting that it may index the increased ‘sense of agency associated with 100% action-effect contingency
	Experiment 5	No difference in Tb amplitude between <i>active</i> and <i>passive</i> conditions However, Tb amplitude smaller when sounds have 100% probability compared to 50% probability sounds
P2 Component	Experiments 1 & 2	Increased P2 amplitude in the <i>active</i> condition relative to the <i>passive</i> condition
	Experiments 3 & 4	P2 amplitude smaller when sounds have 100% probability compared to 50% probability sounds
	Experiment 5	P2 amplitude smaller in the <i>active</i> condition compared to the <i>passive</i> condition Effect of <i>Contingency</i> found for the <i>passive</i> condition P2 scalp distributions were dissimilar for the different <i>Contingency</i> conditions, and P2 latency differences were observed between the <i>active</i> and <i>passive</i> peaks

Figure 5.1. Summary of findings. The figure summarises the main findings across all the five experiments of the thesis, categorised by the ERP components (the N1, Tb, and P2 component). Within each ERP component, findings are separated based on the set of experiments that each finding was located in.

experiments. The two experiments revealed a very similar pattern of results: while there was no evidence of N1 suppression in either experiment (i.e., N1 amplitude was not significantly reduced in the active relative to the passive conditions), we did instead observe suppression of the Tb component in the *active* condition. P2 enhancement in the *active* condition was also found in both experiments. The key point to note is that the primary difference between the *active* and *passive* conditions was that the participant had control over whether the sound occurred in the *active* condition but not the passive condition; that is, they had a sense of agency over the sounds in the *active* condition. Given this, the results suggest that it may be the Tb component, and possibly also the P2 component, that indexes one's sense of agency over sensory events.

In Experiments 3 and 4, we investigated the relation between contingency— operationalised as the probability that the sound would occur following an action— and sensory attenuation. Similar to the first two chapters, in Experiment 3 a willed *inaction* caused sound onset whereas in Experiment 4 the willed *action* caused sound onset. In Experiments 3 and 4, participants' inactions (Experiment 3) or actions (Experiment 4) caused sounds 100% of the time in the *FC* condition, but only 50% of the time in the *HC* condition. In both experiments, we found a reduction in Tb amplitude, but only when the Tb in the *FC* condition was compared to the *HC-inaction* condition (that is, when it was participant inaction that caused a sound in the *HC* condition). We also found P2 suppression in the *active* phase of the *FC* condition relative to both *HC-action* and *HC-inaction* across both experiments. The results suggest that contingency— operationalised in terms of probability— is most likely indexed by the P2 component, but that the Tb component may also play a role.

Lastly, in Experiment 5, we extended the study of contingency to the traditional self-stimulation paradigm. In contrast to the previous experiments, rather than having to make a pre-emptive decision about whether to trigger sounds, participants instead pressed a button

which directly and immediately caused sound onset. In the *active 100* condition, participant button-presses triggered sounds 100% of the time. In the *active 50* condition, participant button-presses triggered sound onset 50% of the time. In the *passive 100* and *passive 50* conditions, participants were instructed to passively listen to sounds that appeared on either 100% of trials (*passive 100*) or 50% of trials (*passive 50*) during the block. In contrast to the results of the previous chapters, we observed N1 suppression in the *active-corrected* condition relative to the *passive* condition and smaller N1 amplitudes for sounds that occurred with a 100% probability compared to sounds that occurred with a 50% probability. The Tb component did not show suppression in the *active* conditions (i.e., to self-produced sounds), but did show a reduction in Tb amplitude when sound onset was 100% relative to 50%, consistent with the results of Chapter 3. The P2 component showed suppression in the *active* condition (i.e., to self-produced sounds), but this analysis was complicated by the fact that the latency of the P2 component in the *active* and *passive* conditions differed substantially, with the P2 component of the *active* condition occurring within the P3 range (Polich, 2012). One possible explanation is that the P2 peaks were obscured by other overlapping components, such as the N2 and P3 components (Michalewski, Prasher, & Starr, 1986; Crowley & Colrain, 2004).

The results of the five experiments help to explicate the relationship between sensory attenuation, sense of agency, and action-effect contingency. In the following sections, I will further elaborate on these issues.

5. 1. Experimental measures of sense of agency

With the exception of Experiment 5, all the experiments in this thesis employed a design adapted from the studies of Whitford et al. (2017) and Jack et al. (2019). The core idea behind this design is that the temporal predictability of the sound and motor-related potentials can be controlled for by having participants make a decision regarding whether or not a

sound will occur, and then imposing a long temporal delay between the decision (and any associated motor-evoked potentials), and the onset of the sound. In the case of Experiments 1 and 2, we were able to isolate agency as a variable by removing motor actions as the cause of the sound (Experiment 1) or by including a lengthy delay (at least 1 s) between the action and the sound (Experiment 2), thereby leaving participant choice (i.e., sense of agency) as the only causal factor for the onset of sounds.

A notable and consistent finding across Experiments 1-4 was that N1 suppression was not observed. We instead identified effects in the Tb component. In Experiments 1 and 2, there was a reduction in Tb amplitude in the *active* condition relative to the *passive* condition. In Experiments 3 and 4, we observed a reduction in Tb amplitude in the *FC* condition relative to the *HC-inaction* condition. We suggest that a likely reason why N1 suppression was not observed was that in the experimental designs of Experiments 1-4, the motor action did not occur at the same time as the sound (Schafer & Marcus, 1973; Hughes et al., 2013). Sensory attenuation has often been conceptualised as a result of comparisons between sensory predictions and sensory feedback in the context of an internal forward model (Miall & Wolpert, 1996; Haggard, 2017). According to this account, efference copies based on motor commands form the basis of sensory predictions—the corollary discharge—that are then compared to the sensory consequences (reafference) of self-generated movements. However, we suggest that the internal forward model did not apply in Experiments 1-4, as either motor actions were not involved (in Experiment 1) or were spaced far apart from the resulting sounds (in Experiment 2). In the experiments that did not require a motor action, feed-forward mechanisms of sensory attenuation were presumably not involved given that these mechanisms are thought to be based on efference copies of motor actions. One potential consequence is that these experiments involved retrospective mechanisms of agency (Synofzik et al., 2008; Haggard, 2017). Retrospective forms of agency involve judgements of

one's agency (what Synofzik et al. (2008) call *judgements of agency*) that are formed due to conceptual, interpretive judgements of a sensory effect being the result of one's actions (or, in this case, inaction) (Synofzik et al., 2008). Although they are usually preceded by phenomenological experiences of agency (what Synofzik et al. (2008) describes as the *feeling of agency*), these two different forms of agency are not necessarily coupled together. For example, it could be that in Experiments 1 - 4, participants had agency over the sounds, and were able to make *judgements of agency*, but perhaps did not experience the same *feelings of agency* that would normally be experienced in a traditional self-stimulation experiment, where motor actions and resulting sounds are closely bound in time.

The results of Experiment 5, which used the traditional self-stimulation paradigm, showed the opposite pattern of results. That is, in Experiment 5 we observed N1 suppression to both *Production* and *Contingency*, whereas we observed Tb suppression only in the case of *Contingency*. The results of Experiment 5 replicated the 'N1 suppression effect' that has been previously reported in the majority of previous studies in the sensory attenuation literature (Bäß, Jacobsen, & Schröger, 2008; Knolle et al., 2012; Horváth & Burgyán, 2013; Hughes et al., 2013; SanMiguel et al., 2013; Saupe et al., 2013; Timm, SanMiguel, Saupe, & Schröger, 2013; Timm, Schönwiesner, SanMiguel, & Schröger, 2014; Oestreich et al., 2016; Neszmeily & Horváth, 2017; Elijah, Pelley, & Whitford, 2018; Seidel, Ghio, Studer, & Bellebaum, 2021). This is likely because N1 suppression is dependent on motor actions and the resulting stimuli to either co-occur, or occur close-in-time to each other, which was the case in Experiment 5 but not Experiments 1-4. So far, very few studies have formally investigated the role of the Tb component in the context of the phenomenon of sensory attenuation. One such study was conducted by SanMiguel et al. (2013). The study involved three conditions normally used in sensory attenuation studies, i.e., the *motor-auditory*, *auditory-only*, and the *motor-only* conditions. The authors of the study also included a manipulation of inter-

stimulus intervals, with three ISI conditions: 0.8s, 1.6s, and 3.2 s across all three *motor-auditory*, *auditory-only*, and the *motor-only* conditions. Participants underwent training blocks to accustom themselves to generating sounds at the requested ISI levels; there was also visual feedback during the experiment to remind participants to generate sounds at the requested ISI levels. The *auditory-only* condition involved replaying the sounds generated in the *motor-auditory* conditions thereby also ensuring equivalent ISIs across conditions. Temporal predictability, however, was not controlled for as there was no visual indication of stimulus timing. The results of the study found Tb suppression only for the longest ISI level (i.e., when the ISI was 3.2 s). However, the authors suggested that the observed Tb suppression might have been due to overlapping of the unspecific component (a N1 subcomponent), rather than ‘true’ suppression of the Tb. Given the lack of systematic inquiry into the Tb component, it would be worthwhile for future studies to further investigate the effects of agency on the Tb in the context of the traditional self-stimulation paradigm.

In Experiments 1 and 2, the P2 component was *enhanced* (rather than suppressed) when participants had agency over sounds. This result differs from most previous studies that have used the traditional self-stimulation paradigm, although it should be acknowledged that these studies did not investigate the role of agency on P2 amplitude specifically (Knolle et al., 2012; Horváth & Burgyán, 2013; Timm et al., 2014; Klaffehn et al., 2019). While the functional significance of the P2 component is not yet very clear (Crowley & Colrain, 2004, Lijffijt et al., 2009), it has been associated with attention and categorization processes (García-Larrea et al., 1992; Crowley & Colrain, 2004, Lijffijt et al., 2009). It has also been linked to working memory processes (Lefebvre et al., 2005; Finnigan et al., 2011; Duzcu et al., 2019).

Relatively few studies have investigated the association between the P2 component and sense of agency specifically (Timm et al., 2016; Seidel et al., 2021). One such study was

conducted by Timm et al. (2016). They implemented a manipulation where participants perceived agency over a sound in one condition (*real-time* condition) but experienced an illusory lack of agency in another condition (*illusion* condition). In the *illusion* condition, participants were repeatedly exposed to a fixed temporal delay of 200ms between button-presses (triggered by a visual cue) and the resulting sounds. The repeated exposures to the 200ms-delayed action-effects would cause participants to acclimate to the delay, shortening the perceived delay. Participants were then exposed to action-effects without any delay in a test trial; this would cause a perceptual illusion wherein effects are perceived to occur before the action. The perceptual illusion has been shown to abolish the sense of agency associated with self-generated sound (when measured by asking participants if they thought they were the agency of a particular sound) (Timm, Schönwiesner, SanMiguel, & Schröger, 2014). Participants in the *illusion* condition directly caused sounds in test trials but reported not experiencing a sense of agency over these sounds. In contrast, participants in the *real-time* condition were not exposed to the temporal delay acclimation underwent by participants in the *illusion* condition, meaning that they retained their sense of agency when they triggered sounds in during the test trials. Their results demonstrated that N1 suppression occurred regardless of whether participants reported a sense of agency over the sounds (*real-time* condition) or not (*illusion* condition). However, they found that P2 suppression was sensitive to reported sense of agency; participants in the *real-time* condition (high sense of agency) showed significantly smaller P2 amplitudes when sounds were self-generated relative to externally generated sounds, while P2 suppression effects were significantly smaller for participants in the *illusion* condition (low sense of agency). Timm et al. (2016) thus concluded that the P2 component might be a suitable marker for the investigation of the subjective sense of agency.

Given the results presented above, one possible hypothesis is that there are different mechanisms that inform the sense of agency – for example, motor prediction vs. retrospective judgements - and that these different forms of agency are indexed by different ERP components. Going further, we could reason that motor-predictive forms of agency are better represented by the N1 component while more ‘cognitively complex’ forms of agency, such as retrospective judgements, are better represented by later components including the Tb and P2 components. There is some experimental evidence to support this assertion. For example, Seidel et al. (2021) conducted a sensory attenuation experiment in which they manipulated participants’ perceived levels of control over sound production by exposing participants to a two-button choice task in which participants were induced to experience either high or low levels of an illusion-of-control (IoC). During the two-button choice task, participants were required to generate sounds which were deemed “desirable” versus sounds that were “undesirable” (labelled as such during the introduction of the experiment). However, participants did not know that in actual fact, their choice of action did not have any influence over which sounds occurred. Rather, in the high IoC condition, “desirable” sounds had a baseline 70% chance of occurring, while in the low IoC condition, the “desirable” sounds had a 30% of occurring. Participants who were exposed to the high IoC condition were thus primed to believe that had more control over their ability to generate “desirable” sounds. Seidel et al. found that while N1 suppression was not affected by participants’ perceived control over sound production (that is, N1 amplitude was lower when sounds were self-generated compared to externally generated sounds regardless of IoC condition), the P2 and P3a components were insofar as suppression of these two components was only observed when participants perceived themselves as having high levels of control over the production of the sound. The authors drew similar conclusions to our own, namely that N1 suppression seems to “*reflect simple predictions directly linked to motor actions and appears unaffected*

by context-dependent variations in agency” (Seidel et al., 2021, p. 2 - 3), while components such as the P2 “*appear to reflect prediction mechanisms sensitive to top-down influences such as context-dependent modulations of subjective agency”* (Seidel et al., 2021, p. 3).

The results of Experiments 1 and 2 suggest that the Tb component might be sensitive to these context-dependent judgements of agency. Whereas the N1 component has been associated with lower-level processing of auditory features such as auditory intensity (Beagley & Knight, 1967; Picton, Goodman, & Bryce, 1970; Adler & Adler, 1989), the Tb and P2 components have been associated with higher cognitive functions such as language, memory, and learning (García-Larrea et al., 1992; Giard et al., 1994; Tonnquist-Uhlen et al., 2003; Shahin et al., 2003; Crowley & Colrain, 2004; Langers et al., 2007; Harpaz et al., 2009; Lijffijt et al., 2009; Hämäläinen et al., 2011; Bruneau et al., 2003; Azouz et al., 2014). If the two different mechanisms that inform the sense of agency (i.e., predictive vs. retrospective mechanisms) can be classified as ‘lower’ and ‘higher’ functions in terms of their cognitive requirements, then it could be hypothesised that different aspects of the sense of agency will map on to different ERP components that differ in terms of cognitive complexity. Related to this idea, one possible future experiment would be to replicate Experiment 2 but to add another condition in which participants must press a button when the fixation and decision lines intersect each other, and the sounds would immediately follow the button press. This condition would retain the action-effect coupling of the classic self-stimulation experiments while also controlling for temporal predictability (essentially creating the *motor-auditory* condition but with different visual stimuli). The experiment would allow comparisons to be made between the sense of agency associated with the motor-action *per se* (i.e., corollary discharge related mechanisms) from the more ‘cognitive’ sense of agency associated with making the decision about whether to hear the sound.

Most experiments studying sensory attenuation have argued that the phenomenon is underpinned by corollary discharges (Hughes et al., 2013; Horváth, 2015) and so, by extension, have conceived of agency only in its predictive form. However, recognising that the sense of agency is also informed by judgements and cognition will allow for a deeper exploration of the relationship between sensory attenuation and sense of agency. An example of one such study that has taken this approach is the study of Desantis, Weiss, Schütz-Bosbach, and Waszak (2012). In their behavioural study, participants sat alongside a confederate, in which their views of each other were obstructed by a piece of cardboard. Both the participant and confederate observed a screen that displayed a clock face. This clock face designated the time frame in which the participant and confederate had to simultaneously press a button to generate a sound. Participants were led to believe that either they or the confederate were responsible for the sound generation by means of a name that was presented at the top of the screen at the start of each trial. The name at the top of the screen would supposedly indicate who was responsible for sound generation. In reality, however, all sounds were created by the participant. After presentation of the initial sound, a second sound was presented shortly after that varied in volume. The experimenters measured sensory attenuation by instructing the participant to judge whether the sound that was first generated was either louder or softer than the following one. The results showed that when sounds were self-generated, participants perceived the volume of the sound to be attenuated compared to the subsequent ‘control’ sound, in contrast to when the sound was supposedly generated by the confederate. The results of this study further demonstrate that sensory attenuation is not only a predictive phenomenon based on motor mechanisms but can also be influenced by a person’s beliefs and judgements of agency.

The preceding discussion has outlined the different mechanisms that inform one’s sense of agency, and of various ways in which sense of agency can be examined. Although

past studies have typically conflated motor-predictive sensory attenuation with the sense of agency, the results of Experiments 1 and 2 demonstrate that agency is dissociable from motor-related mechanisms and can be indexed by different ERP components. Future studies could be directed towards investigating the boundaries between the different neural processes that contribute towards agency and its relationship to different ERP components, such as the aforementioned study of Seidel et al. (2021).

In the following section, I will discuss the role of action-outcome contingency in the phenomenon of sensory attenuation.

5. 2. Action-effect contingency in the context of sensory attenuation

Experiments 3 – 5 explored the role of contingency – operationalized as probability of a sound occurring following an action – in sensory attenuation. Experiments 3 and 4 used an experimental methodology closely resembling that of Experiments 1 and 2, whereas Experiment 5 used the ‘self-stimulation’ paradigm that has been most commonly used in studies of sensory attenuation (e.g., Schafer & Marcus, 1973; Curio et al., 2000; Bäß et al., 2008; Knolle et al., 2012; Horváth & Burgyán, 2013; SanMiguel et al., 2013; Saupe et al., 2013; Elijah et al., 2018; Neszmeilyi & Horváth, 2017; Oestreich et al., 2016).

In Experiments 3 and 4, participants’ actions (i.e., whether willed inactions in Experiment 3, or willed button-presses in Experiment 4) caused sounds to be presented at either 100% contingency (i.e., the action elicited a tone 100% of the time; the *FC* condition) or 50% contingency (i.e., the action elicited a tone 50% of the time; the *HC* condition). A similar pattern of results was observed across the two experiments: while there was no difference in N1 amplitude between the *FC* and *HC* conditions, we did observe suppression of both the Tb and P2 components in the *FC* condition, relative to the *HC* condition.

The N1 component has previously been shown to index surprise, or prediction error, with more surprising tones eliciting N1 amplitudes that were more negative (Schafer et al., 1981; Bendixen, SanMiguel, & Schröger, 2012; SanMiguel et al., 2013; Timm et al., 2013). Given that fact that the occurrence of sounds in the *HC* conditions were more surprising than the occurrence of sounds in the *FC* condition, we were somewhat surprised (no pun intended) that we did not observe a between-condition difference for the N1 component. One explanation for this result may be due to the long ISIs across both experiments (~10 s on average). Although lower sound probability (and hence higher prediction error when a sound does occur), normally result in N1 amplitudes that are more negative when compared to sounds with higher probabilities, the long ISIs may have given participants time to prepare cognitive resources to accommodate for the uncertainties of sound onset. For example, in a study by Polich (1990) investigating the P3 component, participants listened to a stream of 1000 Hz tones with random presentations of a 2000 Hz target tone, which participants had to identify via a finger tap. The chance of a 2000 Hz target tone appearing was either 20% or 80%, depending on the condition. The results, as reported by Polich (1990), demonstrated enhanced P3 amplitudes for target sounds of 20% probability compared to target sounds of 80% probability during low ISI conditions (about 2 – 3 s) but not during high ISI conditions (about 4 – 10 s). The study by Polich (1990) can thus be adapted to investigate the relationship between ISIs and probability for the N1 component.

It is worth noting that while action-outcome probability was the subject of study in Chapters 3 and 4, these experiments only used contingency levels of 100% and 50%. There are several issues related to this design that are worth noting. Firstly, this design does not assess probability on multiple levels (e.g., 100%, 75%, 50% and 25%), which may help to address whether there is a direct correlation between probability levels and auditory suppression or component amplitude. Secondly, by setting the uncertain probability at 50%, it

does not allow for priors towards one outcome to be formed, as the likely occurrence of sounds did not lean towards ‘tends to appear’ vs. ‘tends not to appear’. Without such a prior, prediction errors are less likely to be formed. Studies that have investigated the effect of probability of auditory processing have generally used probabilities such as 10% vs. 90% or 20% vs. 80% (Polich, 1990; Pincze et al., 2002; Pereira et al., 2014). Using the example of 10% vs. 90%, when the probability of a sound occurring is 10%, then participants generally expect the sound not to occur; when the probability is 90%, the general expectation is that the sound will mostly occur. Future studies should therefore include more contingency conditions that will examine a broader range of probabilities (this was not done in the present set of studies due to time constraints that would occur in a within-subjects design).

When assessing the effect of contingency in the context of sensory attenuation, another relevant issue is the experimental paradigm itself. For example, recall that in the self-stimulation experiment, participants were required to press a button, with a sound following immediately after the button press. As argued by Horváth (2013), sensory attenuation in humans is often studied in laboratory settings, divorced from the everyday environment. One consequence of this is that we tend to ignore action-effect bindings that we carry over from our everyday lives. One such instance of an action-effect binding (or ‘prior’) that may potentially carry over from everyday life into the laboratory environment is the association between key presses and sounds. In other words, before the experiment has already started, participants may have had a strong prior of *“I expect a sound to immediately follow my button press”* brought about by the *“extensive training through the widespread use of keypress-based interfaces in everyday devices”* (Horváth et al., 2012, p. 1929). The existence of such a ‘prior’ may help to explain why there were no effects of *contingency* for the N1 component in Experiments 3-4, while there was an effect of *contingency* for the N1 component in Experiment 5. In Experiment 5, participants pressed a button that immediately

resulted in a sound following the action. It is arguable that even in conditions where contingencies were set at 50%, participants may have had a strong prior towards “*a sound will likely follow immediately from my button press*”, simply because of their everyday experience. This could explain why, in Experiment 5, 50% probability sounds elicited N1 amplitudes that were more negative than 100% probability sounds because participants implicitly overestimated the probability of sounds occurring from their button-presses, thus causing more prediction errors, which is known to cause more negative N1 amplitudes (as an aside, one possible method of overcoming ecological priors is by exposing participants to training blocks so they become acclimated to certain probabilities) (Roth et al., 1976) In Experiments 3 and 4, participant actions (or inactions) did not immediately result in a sound; that is, the sound occurred after a lengthy delay of at least 1 second. One potential consequence of this novel context is that participants might not have had such strong ‘priors’ regarding the association between willed-button presses and delayed sounds, as this association is less likely to occur in everyday life. In this case, the contingency probabilities in Experiments 3-4 (i.e., 100% vs. 50%) may not have been not affected by these ‘naturally acquired’ associations. This may help to explain why it is the results of Experiments 3 and 4 did not show any effect of *contingency* on N1 amplitude, in contrast to the *contingency* results observed in Experiment 5.

The results of the Tb component analyses were consistent across Experiments 3-5. However, the results of the P2 component analysis differed between Experiments 3-4 and Experiment 5. The Tb results of Experiments 3 and 4 showed a reduction in Tb amplitude only when sounds with 100% probability (*FC* condition) were contrasted against 50% sounds that were elicited by inaction (*HC-inaction* condition). The P2 component in Experiments 3-4 showed suppression for 100% sounds when contrasted with both types of 50% sounds. In Experiment 5, there was no Tb suppression of the *active* Tb relative to the *passive* Tb for the

Production manipulation but there was reduction in Tb amplitude for 100% sounds compared to 50% sounds for the *Contingency* manipulation, consistent with the results of Experiments 3 and 4. Likewise, the P2 component also reflected suppression for 100% sounds compared to 50%. Interestingly, however, the latency of the P2 component of the *active* and *passive* conditions differed substantially, with the *active* condition ostensibly not having a P2 peak, but rather a peak in the P3 range (Polich, 2012). Given that the P2 is an obligatory component of the auditory-evoked potential (Näätänen & Picton, 1987; Crowley & Colrain, 2004; Wagner et al., 2013), one possible explanation is that the P2 peaks were obscured by other overlapping components, such as the N2 and P3 components. However, this argument is weakened by the fact that there is no evidence of a N2 wave, so the existence of a N2-P3 complex obscuring the P2 component is unlikely.

In Experiments 3 and 4, Tb suppression was only significant when comparing the *FC* condition to the *HC* sounds triggered by the willed inaction (*HC-inaction*); the effect was not significant when comparing *FC* sound to *HC* sounds triggered by action (*HC-action*). While the reasons for this discrepancy are not clear (though it might be too extreme to call it a discrepancy, because supplementary analyses showed no differences in Tb amplitudes between *HC-action* and *HC-inaction*), one possible reason is that participants found sounds generated via inaction to be more unusual, so that sounds generated by inaction demanded more attention and thus more neural resources to process than sounds generated by action. Given that increased attention has been shown to increase the amplitude of the N1 and Tb components (Timm et al., 2013), it would be worthwhile investigating whether there are any systematic effects of inaction in relation to attention. For Experiment 5, although there were effects of *Contingency*, we found no effect of *Production* (that is, no difference between the *active* and *passive* conditions) for the Tb component. The fact that we did not observe an effect of *Production* for the Tb component in Experiment 5 was somewhat surprising (to us,

at least), given that we have argued that this component may index a participant's sense of agency. Participants in Experiment 5 ought to have been able to form top-down judgements of agency over sounds they generated, particularly given that their motor actions immediately resulted in a sound. Given our aforementioned suggestion that the Tb component is a likely marker for such top-down judgements of agency, one might have expected to see Tb suppression of the *active* condition relative to the *passive* condition.

The P2 component had identical results across Experiments 3 and 4; the *FC* condition showed suppression effects when compared to the *HC* condition. Since the P2 component has been associated with attention, memory, and learning (García-Larrea et al., 1992; Crowley & Colrain, 2004; Lijffijt et al., 2009), one possibility is that the increased P2 amplitude in the *HC* conditions may be due to increased neural processing of sounds occurring under uncertain conditions. The reason why we observed reduced P2 amplitudes in the *FC* condition relative to *both HC* conditions – a result which differed from the Tb component – may potentially be suggestive of motor processes being involved in the Tb component. For example, some studies using the self-stimulation design have demonstrated Tb suppression when sounds were self-generated compared to when they were externally generated (SanMiguel et al., 2013; Horváth, 2013), although neither of the studies controlled for the issue of temporal predictability. In Experiment 5, we found reduced P2 amplitudes in the *100* condition compared to P2 amplitudes in the *50* condition. However, there was no effect of *Production* in the P2 component. Furthermore, we found latency differences between the P2 components of the different production conditions. P2 components in the *passive* conditions showed earlier P2 responses compared to those in the *active* conditions. One potential reason for this is an overlap in the P2, N2, and P3 components caused by differences in the probability of sound occurrence (Michalewski et al., 1986; Crowley & Colrain, 2004). In light of these complex results, we suggest that future studies of sensory attenuation would do

well to expand the components-of-interest beyond the traditional focus on N1, and include other components including, but perhaps not limited to, the Tb and P2 components.

5. 3. Sensory attenuation and schizophrenia

Some of the first-rank symptoms of schizophrenia, such as delusions of control and certain types of auditory hallucination (e.g., audible thoughts), have been argued to reflect a deficit in agency attribution (Ford et al., 2001; Ford & Mathalon, 2004, 2005; Heinks-Maldonado et al., 2005; Ford et al., 2007). As mentioned in Chapter 1, patients with schizophrenia have been consistently found to show subnormal levels of sensory attenuation compared to healthy participants. For example, numerous studies have shown that patients with schizophrenia do not demonstrate the same level of N1 suppression compared to healthy participants, either when producing sounds directly by vocalizing (i.e., in the Talk-Listen task), or when producing sounds indirectly via other motor actions such as when pressing a button to elicit a tone (Ford et al., 2001; Ford & Mathalon, 2004, 2005; Heinks-Maldonado et al., 2005; Ford et al., 2007). Given that N1 suppression has long been assumed to reflect the actions of corollary discharges and related mechanisms, the implication is that patients with schizophrenia demonstrate deficits in the internal forward model (Ford et al., 2001; Ford & Mathalon, 2004, 2005; Ford et al., 2007). It has also been suggested that the psychotic symptoms experienced by patients with schizophrenia (i.e., commonly, these include delusions and hallucinations) may be informed by both perceptual and cognitive mechanisms at different levels of a neurophysiological hierarchy (Fletcher & Frith, 2008).

Previous studies investigating sensory attenuation in schizophrenia populations have been based on principles of corollary discharge, and thus have most commonly assessed motor-predictive forms of agency (Ford et al., 2001; Ford & Mathalon, 2004, 2005; Heinks-Maldonado et al., 2005; Ford et al., 2007). However, as previously discussed, agency, as a multi-faceted phenomenon, is likely to be underpinned by several different processes,

including motor-based predictions, but also incorporating higher-order ‘inferential’ processes (Synofzik et al., 2008; Haggard, 2017; Seidel et al., 2021). As the majority of previous studies have only investigated the former aspect of agency in the context of sensory attenuation, it is fair to say that we do not, as yet, have a full understanding of the nature and extent of the deficits in agency experienced by people with schizophrenia. The experimental designs employed by Experiments 1-2 of the present thesis would potentially allow for top-down ‘judgements of agency’ to be assessed in patients with schizophrenia. Specifically, if the Tb component is indeed a suitable index for top-down judgements of agency, then we would predict that patients with schizophrenia would also show deficits in Tb suppression in the *active* relative to the *passive* condition in this experimental task.

5. 4. Limitations and future directions

The experimental design utilized in the first four experiments in this thesis differ significantly from those used in previous studies of sensory attenuation (Curio et al., 2000; Bäß et al., 2008; Knolle et al., 2012; Horváth & Burgyán, 2013; SanMiguel et al., 2013; Saupe et al., 2013; Elijah et al., 2018; Mifsud et al., 2016; Neszmeélyi & Horváth, 2017; Oestreich et al., 2016). One of the differences between the designs used in this thesis and those in the previous literature is the difference in ISIs between the experimental paradigms. This is important as different ISIs can influence ERP component magnitudes (SanMiguel et al., 2013; Horváth, 2015). An important point to note is that the N1 is not a unitary component; in contrast, there are believed to be at least three subcomponents for the N1 (Näätänen & Picton, 1987; Horváth, 2015). The N1 component is itself largely influenced by the ISIs in the given experiment. When sounds are presented in short ISIs (< 4 s), the N1 component is dominated by a more frontal or fronto-central source (Horváth, 2015). However, when sounds are presented in long ISIs (> 5 s), the observed N1 component is dominated by a centrally maximal subcomponent also known as the non-specific N1

component. The non-specific N1 component is believed to be modality free, meaning that it is not specific to auditory stimuli (Davis & Zerlin, 1966; Hari et al., 1982; SanMiguel et al., 2013) (Lehtonen, 1973).

Most previous experiments investigating auditory N1 suppression have done so using ‘short’ ISIs of less than 5 seconds on average (Curio et al., 2000; Bäß et al., 2008; Knolle et al., 2012; Horváth & Burgyán, 2013; SanMiguel et al., 2013; Saupe et al., 2013; Elijah et al., 2018; Mifsud et al., 2016; Neszmeélyi & Horváth, 2017; Oestreich et al., 2016). In contrast, Experiments 1 – 4 of the present thesis used ISIs that were much longer than this: approximately 10 seconds on average. As discussed above, the significance of this is that different N1 subcomponents that are assumed to reflect different sensory processes are ‘triggered’ by different ISIs. The frontal/fronto-central N1 subcomponent is generally regarded as a marker for auditory event- and feature-detection processes (Näätänen & Winkler, 1999, Horváth, 2015), while the non-specific N1 reflects processing of the conscious detection and orientation towards a modality-free sensory event (Horváth, 2015; SanMiguel et al., 2013). The fact that the two different experimental paradigms have different ISIs mean that there is a strong possibility that they could be indexing different processes. One way of addressing this in future research would be to use and compare a variety of different ISI levels in the context of the present experimental design. Furthermore, future source localization studies should also investigate the implications of frontal versus temporal generators of the ERP components examined in this thesis (such as the implications of the differences between the N1 and Tb components).

The role of readiness potentials in sensory attenuation is also worth considering, especially in the context of action-effect contingency. The readiness potential is a slow, negative-going component that occurs in the second-or-so prior to the initiation or preparation of a movement (Reznik, Simon, & Mukamel, 2018; Vercillo, O’Neil, & Jiang,

2018; Pinheiro et al., 2020). It should also be noted that the readiness potential has also been demonstrated to occur prior to the production of purely mental actions (Alexander et al., 2016; Whitford et al., 2017). There are some studies that have shown that readiness potentials play a significant role in N1 suppression (Reznik et al., 2018; Vercillo et al., 2018; Pinheiro et al., 2020). Reznik et al. (2018) found that the amplitude of the readiness potential to be significantly more negative in the *motor-auditory* condition compared to the *motor-only* condition, suggesting that different forms of expectations are represented in readiness potentials. In another example, Pinheiro et al. (2020) found that the amplitude of readiness potentials to be larger for button-presses with expected sensory feedback than button-presses without expected sensory feedback. This was true whether the expected sensory feedback was actual (the button-press resulted in a real sound) or imaginary (that is, participants were told to imagine the auditory feedback that would follow the button-press). Therefore, the role of readiness potentials in sensory attenuation can make for a compelling research direction, whether in the context of using inaction to generate sounds or in the context of investigating sensory contingencies.

5. 5. Conclusion

In summary, the present thesis attempted to explore the effect of sense of agency and action-effect contingency on the phenomenon of sensory attenuation. To do this, we used a modified experimental protocol that was designed to minimize the effect of motor potentials and control for between-condition differences in temporal predictability. The results revealed that the concept of agency itself is multifaceted and warrant further research in the sensory attenuation literature. Agency is not merely a concept governed by motor processes but also a disposition that the human agent can consciously recognise. The results show that these aspects of agency can be differentiated across different neurophysiological signatures. Likewise, the results showed that action-effect contingency affected not only the perception

of agency but also mediated the effect of sensory attenuation. Given the important role that action-effect contingencies have in ecological settings, this should warrant further research in the future not only for action-effect contingencies but perhaps other ecological considerations. In summary, this thesis has contributed to our understanding of the role agency and contingency plays in sensory attenuation and will hopefully pave the way for other novel explorations of this fascinating phenomenon.

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