Attention, prediction and sensory attenuation: A neurophysiological investigation of the internal forward model

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Attention, prediction and sensory attenuation:

A neurophysiological investigation of the internal forward model

Anthony W. Harrison

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Abstract

The term ‘sensory attenuation’ describes a reduction in the subjective intensity of self-generated stimuli, and accompanying neurophysiological response, compared to those produced externally. Mechanisms underlying this phenomenon are believed to facilitate the distinction between self- and externally-generated events. Accordingly, dysfunction in sensory attenuation has been associated with symptoms involving the misattribution of perceptual experience in people with schizophrenia. Internal forward models of sensory attenuation propose that self-generated stimuli are suppressed based on predictions derived from the motor commands through which they are produced. However, much of the research into sensory attenuation has been subject to methodological confounds that limit conclusions with respect to its underlying mechanisms. Other factors, such as the role of attention, have not been thoroughly explored. This thesis presents the results of four electrophysiological studies that examined factors influencing sensory attenuation, while assessing and controlling for confounding effects. Sensory attenuation was explored through examination of the auditory N1 component of event-related potentials (ERPs), which is believed to reflect the primary cortical response to sound stimuli. Related effects were assessed based on ERP components representing motor preparation, sensory gating, attention, and error monitoring. Our results suggest that temporal predictability reduces N1 amplitudes in a manner that may often account for documented effects, while temporal control amplifies these such that the phenomenon of sensory attenuation is counteracted for stimuli that result from volitional (i.e., self-paced) movement (Chapter 2). Subsequent analyses revealed an interaction between inter-stimulus intervals and this ‘volitional enhancement’, such that shorter intervals increase its effects (Chapter 5). The results of our investigation indicate that action-effect contingency does not influence the amplitude of auditory N1 components (Chapters 3 and 4). Instead, our findings support the notion that sensory attenuation may involve effects relating to attentional suppression (Chapter 3) and control (Chapter 4). These findings provide important insights into the mechanisms underlying sensory attenuation, and implications for future research into the causes and potential treatment of schizophrenia.

Contents

List of Figures

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

1. General introduction

The sensory receptors that an organism uses to monitor change in its environment also provide passage to an array of information reflecting the effects of its own activities. To support an informative perceptual experience, it is important that these competing interpretations regarding the source of sensory information are accurately distinguished (von Holst & Mittelstaedt, 1950). Tactile sensations that are generated as we swim through water or slide our hand along a banister, for example, are more usefully interpreted as the outcome of our movement through the world than movement of the world past us. Similarly, saccadic eye movements that result in a dramatic shift in the reference point of visual information are more appropriately experienced as having resulted from the movement of one’s eyes than the revolution of a scene around us. In addition to supporting perceptual orientation, the capacity to distinguish between self- and externally-generated sensation is important to identifying potential threats in our surrounds. For example, differentiating the sound of our own footsteps from those of someone approaching from behind ensures that we are attuned to any risk this may present. In this way, an essential function of our perceptual system is its capacity to distinguish between self- and externally-generated sensation.

1.1 Corollary discharge mechanisms

The challenge of distinguishing self- and externally-generated sensations was addressed by von Holst and Mittelstaedt (1950), who proposed that duplicates of motor commands (i.e., “efference copies”) are produced within the primary motor cortex and serve to modify incoming sensory information that result from our own movements. In particular, von Holst and Mittelstaedt (1950) proposed that efference copies are used by an organism to modulate and therefore distinguish sensory “reafference” (i.e., incoming sensory material that derives from an organism’s own motor activity) from “exafference” (i.e., that portion resulting from stimuli that are generated by external events). Sperry (1950) used the term "corollary discharge" to describe the mechanisms by which this distinction takes place. It is believed that incoming sensory information may be influenced by corollary discharge at a variety of levels within the perceptual hierarchy, with modulation of reafferent signal associated with differing effects depending on the processing stage that is influenced (Crapse & Sommer, 2008).

Various examples of corollary discharge have been identified across the animal kingdom (see Crapse & Sommer, 2008). One such example is provided by the spiny dogfish, which has mechanosensitive hair cells distributed along its dorsal surface that are used to alert the dogfish to nearby predators and prey. When swimming, the movement of water past these mechanoreceptors provides stimulation in a manner that may be equivalent to the displacement of water by another creature (Harris & Bergeijk, 1962). To avoid confusion, incoming sensory information from these receptors has been found to be inhibited during movement (Roberts & Russell, 1972). In this manner, spiny dogfish are provided with enhanced capacity to detect predators and prey while stationary, and suppress self-generated stimulation to avoid confusion during movement.

Another example of corollary discharge is provided within the neural circuitry supporting auditory perception in *Gryllidae* (i.e., crickets). Crickets communicate with one another through sound that is produced by rubbing their forewings together. The distinct chirping sound that results from this action is generated within millimetres of the cricket's hearing apparatus, including the tympanate membrane, which is situated towards the top of their forelegs (see Hoy & Robert, 1996). To prevent desensitization and remain sensitive to externally-generated sound, the cricket has been found to inhibit incoming auditory signals in a manner that is synchronous to activity in motor neurons generating wing movement and associated sound (Poulet & Hedwig, 2006). As with the spiny dogfish, the cricket is provided with an adaptive advantage by inhibiting the intake of sensory information during activities that produce large quantities of reafferent signal.

A third, more sophisticated, example of corollary discharge use is provided by the *Poephila guttata (*i.e., a type of songbird). Following passive observation of a more mature bird's vocalisations, songbirds have been found to use an iterative process involving comparison of reafferent signal (i.e., self-generated sounds) with memories of the songs produced by others (Margoliash, 1997). These memories are represented within corollary discharge and support the fine-tuning of vocal production based on error signals that are generated when the produced sound deviates from recollections of the intended song (Troyer & Doupe, 2000). In this way, the songbird provides an example of corollary discharge involvement in higher-level functions such as planning and learning through observation (Crapse & Sommer, 2008).

1.2 Sensory attenuation

Another phenomenon that has been attributed to corollary discharge mechanisms is that of "sensory attenuation". This term is used to describe an observed *reduction* in the subjective intensity and neurophysiological response to sensations that have been self-generated, compared with identical sensations when produced externally (e.g., Blakemore et al., 1998; Schafer & Marcus, 1973). The inability to tickle oneself provides a classic example of sensory attenuation that is relatable to any reader. Studies have demonstrated that the ticklishness of sensations produced using a mechanical arm to stimulate participants' palms (i.e., quantified on the basis of self-report using Likert scale) is reduced when stimuli are self-generated, compared with those produced automatically or by an experimenter (Blakemore et al., 1999; Blakemore et al., 2000). These effects parallel findings obtained through functional magnetic resonance imaging (fMRI), which have demonstrated reduced activation in the somatosensory cortex for self-generated tactile sensations compared with those produced externally (Blakemore et al., 1998). While acknowledging the implied assumption that stimulus intensity is associated with ticklishness, these findings appear to implicate sensory attenuation in the reduced ticklishness of self-generated touch.

Further evidence of the reduced intensity of self-generated tactile sensations is provided by research examining participants' estimates of the forcefulness of tactile pressure. Research by Bays et al. (2005) examined participants' estimates of pressure applied to their fingers by a mechanical device. They observed a reduction in the perceived forcefulness when the level was determined by their synchronous press of a force sensor than when generated in the absence of participant input. Together, these findings suggest that corollary discharge mechanisms support a reduction in the perceived intensity of self-generated tactile sensation.

Research has also examined effects of sensory attenuation within the auditory domain. In an early example, Suga and Shimozawa (1974) examined auditory processing in bats based on direct measurement of activity at electrodes placed within the auditory nuclei. Their findings demonstrated reduced cortical activation in this region during the production of vocalisations, compared with levels observed in response to recordings of the same sounds. In another example, Eliades and Wang (2008) used an array of electrodes to investigate the suppression of auditory cortical response in marmoset monkeys. They observed a reduction in the rate of firing in response to self-generated vocalisations when auditory feedback was unaltered, compared to that observed when the pitch of auditory feedback was altered. This suggests that the cortical response was reduced when the observed auditory stimuli matched those that participants anticipated, relative to the cortical response when they did not. Other research has examined sensory attenuation based on neurophysiological activity, including through electroencephalography (EEG; reflecting changes in electrical potential on participants' scalps) and magnetoencephalography (MEG; reflecting changes in the magnetic fields generated by neural activity). These studies have explored attenuation of the neurophysiological response to sound based on action-stimulus pairings that are specific to the experimental setting, including computer-generated tones triggered by finger and leg movements (e.g., Martikainen et al., 2005; Mifsud et al., 2018; Mifsud et al., 2016; van Elk et al., 2014). In this way, sensory attenuation has been observed across a variety of action types and sensory modalities.

1.3 The internal forward model

Sensory attenuation is believed to be supported by an 'internal forward model' (IFM), in which efference copies are used to suppress predictable self-generated sensations (Miall & Wolpert, 1996; Wolpert, 1997; Wolpert et al., 1995). In the context of sensory attenuation, the term "corollary discharge" has been used to describe the prediction that is generated within sensory cortices on the basis of an efference copy and compared against actual sensory experience (Ford & Mathalon, 2012). Although the neurological site of this comparison remains a subject of investigation, the cerebellum has been identified as a potential candidate (Blakemore et al., 1998; Cao et al., 2017). According to the IFM account, sensory information that is predicted on the basis of one's motor activity is filtered out of the incoming signal so that processing may prioritise stimuli resulting from externally-generated events (see Fig. 1.1).

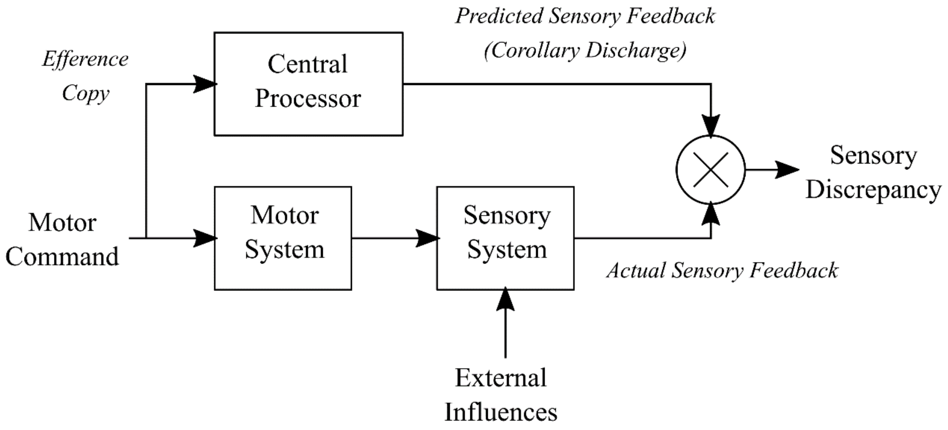

Fig. 1.1. The internal forward model of motor control. Adapted from Miall and Wolpert (1996).

According to the IFM framework of sensory attenuation, the suppression of self-generated sensations depends on their predictability. The role of prediction in sensory attenuation has been supported by research demonstrating that perturbation of relatively innate stimuli resulting from one’s motor activities (i.e., those arising directly as a result of one’s action, such as self-touch and vocalisations) reduces the level of sensory attenuation. For example, temporal and spatial alterations to tactile stimuli have been found to increase the ticklishness of self-generated actions (Blakemore et al., 1999). Similarly, pitch-shifting or delaying auditory feedback has been shown to reduce attenuation of the neurophysiological response to one’s own vocalisations (Behroozmand & Larson, 2011; Behroozmand et al., 2011; Heinks-Maldonado et al., 2005). Within the visual domain, Cardoso-Leite et al. (2010) observed a reduction in participants’ sensitivity to detect the orientation of Gabor patches when the presentation of these stimuli were triggered by actions with which they have previously been associated. In accordance with the IFM framework, these findings therefore support an attribution of the sensory attenuation phenomenon to suppression of reafferent signals based on one’s predictions regarding the outcomes of motor activity.

1.4 Electrophysiological studies of sensory attenuation

A variety of studies have used EEG and MEG to explore sensory attenuation in humans through examination of the cortical response to stimuli. EEG studies have focused on the auditory N1, while the equivalent N1m/M100 has been explored in studies using MEG. These large components occur approximately 100 ms following sound onset and comprise subcomponents originating in the supratemporal plane and superior temporal gyrus, as well as the motor cortex and cingulate gyrus (see Giard et al., 1994; Näätänen & Picton, 1987; Zouridakis et al., 1998). The largest subcomponent, the N1b (McCallum & Curry, 1980; Woods, 1995), has a frontocentral peak and holds particular relevance to understanding corollary discharge mechanisms for at least two reasons. Firstly, the N1b is believed to originate in the primary auditory cortex (Zouridakis et al., 1998). Secondly, the magnitude of the N1b has been shown to be intensity-dependent. Louder sounds, for example, have been found to elicit larger auditory N1b amplitudes when all else is held equal (see Mulert et al., 2005). This suggests that the amplitude of the N1b (described henceforth simply as the N1) is likely to reflect the salience of stimuli within one's perceptual experience (Whitford, 2019).

Electrophysiological investigations of sensory attenuation to self-generated sounds have relied on two general experimental designs: namely 'talk-listen and 'press-listen' paradigms. Talk-listen paradigms have explored differences in the response of the auditory cortex to self- and externally-generated speech (e.g., Creutzfeldt et al., 1989; Curio et al., 2000; Ford, Mathalon, Kalba, et al., 2001). In these, a sequence of vocalisations is generated and channelled into participants' headphones. The evoked potential to each vocalisation is considered to represent processing of self-generated speech sound. Recordings of these vocalisations are taken and subsequently played to participants, while they listen passively. In this condition, evoked potentials were taken to represent the processing of externally-generated speech that was identical to sounds produced during active vocalisation. These studies have demonstrated an apparent reduction in the N1 (and equivalent MEG component) of the evoked response to self-generated sounds, compared with those produced externally (Curio et al., 2000; Ford, Gray, et al., 2007; Ford, Mathalon, Kalba, et al., 2001; Heinks-Maldonado et al., 2005; Houde et al., 2002).

At least two methodological confounds limit the conclusions drawn based on talk-listen paradigms. Both relate to the effects associated with differences in movement between conditions (i.e., talking or passively listening) and difficulty dissociating these effects from those associated with self-generation per se (i.e., whether self- or externally-generated). Firstly, artifacts associated with either activity within motor cortices or overt movement of muscles controlling the jaw or vocal apparatus may affect the evoked potential during self-generation conditions (Horváth, 2015; Hughes et al., 2013b). Secondly, muscles within the middle ear are known to contract during vocalisations in a manner that attenuates the transmission of sound to the inner ear (Borg & Zakrisson, 1975). This contraction, known as the stapedius reflex (Wever & Bray, 1937; Wever & Bray, 1942), is also elicited in response to sounds in excess of 20dB and is believed to protect hearing apparatus from exposure to potentially damaging sound (Borg, 1968; Teig, 1973). While the resulting suppression of sound may appear consistent with the sensory attenuation phenomenon, the effect of these anatomical mechanisms is difficult to disentangle from proposed neurophysiological processes contributing to the suppression of self-generated stimuli.

In light of methodological limitations to the talk-listen paradigm, press-listen paradigms have examined effects involving forms of self-generated sound for which other variables may be more accurately controlled. This is in recognition of the diverse range of auditory stimuli that an individual may produce on a daily basis, including the sound of footsteps on pavement or a pen tapping against a desk. In press-listen paradigms, participants are instructed to press a keyboard button repeatedly. In ‘active’ conditions, each button press will elicit a sound (e.g., pure tones) via participant headphones. In a separate ‘motor’ condition, participants will undertake the same activity except that button-presses will not elicit sound stimuli. By subtracting the evoked ‘motor’ potential from that of the ‘active’ condition, a ‘motor-corrected’ auditory evoked potential is produced. Evoked potentials in this condition are taken to reflect the cortical response to self-generated stimuli, controlling for muscle artefacts and other activity associated with motor production. Sequences of self-generated tones are then played back to participants while they passively listen. Evoked potentials in this condition are taken to reflect the processing of an identical stimulus that has been externally-generated. In an MEG study utilising the press-listen paradigm, Martikainen et al. (2005) demonstrated a reduced N1m to self- versus externally-generated sound following correction for motor activity. Subsequent research has consistently replicated this finding, demonstrating a reduced neurophysiological response to self-generated sound compared with passively observed sound, including after motor-correction (Aliu et al., 2009; Baess et al., 2011; Bäß et al., 2008; Bednark et al., 2015; Cao et al., 2017; Ford et al., 2014; Hughes et al., 2013a; Lange, 2011; Mifsud et al., 2016; Sanmiguel et al., 2013; Sowman et al., 2012; Timm et al., 2013; Timm et al., 2016; Whitford et al., 2011).

1.5 Methodological confounds to press-listen investigations

Research has sought to distinguished sensory attenuation from suppression based on other features known to influence the magnitude of neurophysiological response to stimuli. In a comprehensive review, Hughes et al. (2013b) delineated evidence of sensory attenuation relating to motor prediction (i.e., predicting the nature of an event based on one’s own actions) from the effects of temporal predictability and control, as well as non-motor prediction and attention. Based on this review, Hughes et al. (2013b) concluded that the paradigms used to study sensory attenuation leave open the possibility that each of these effects may contribute to observed differences between self- and externally-generated sensations. In the following sections, I provide a summary of findings with respect to each.

1.5.1 Temporal predictability

When self-generated stimuli result more-or-less instantaneously from an individual’s motor activity, the timing of these stimuli are predictable to that person. In contrast, the temporal predictability of externally-generated stimuli may be supported by cues indicating the impending onset or may not. A variety of studies have demonstrated that increasing the temporal predictability of externally-generated stimuli reduces its neurophysiological response and corresponding subjective intensity (Lange, 2009; Schafer & Marcus, 1973; Schwartze et al., 2011; Sowman et al., 2012; Vroomen & Stekelenburg, 2010; Weiskrantz et al., 1971). In an experiment by Lange (2009), sequences of tones were presented with a consistent interval of 550 ms or with an inconsistent interval (i.e., varying between 300 ms and 800 ms) that had a mean of 550 ms. Lange (2009) examined event-related potentials (ERPs) generated by tones presented following a 1650 ms delay after each sequence. The amplitude of N1 components elicited by temporally predictable stimuli (i.e., those following sequences with consistent intervals) were found to be reduced in comparison to those that were unpredictable (i.e., those following sequences with inconsistent spacing). The results of this investigation corroborate earlier studies demonstrating that increased temporal predictability is associated with a reduction in auditory N1 amplitude (Schafer & Marcus, 1973; Weiskrantz et al., 1971).

Several recent studies have attempted to control for effects associated with temporal predictability in the sensory attenuation phenomenon (Kaiser & Schütz-Bosbach, 2018; Klaffehn et al., 2019; Sowman et al., 2012). In an investigation by Sowman et al. (2012), ERPs resulting from self-generated tones were compared with those produced by externally-generated stimuli that varied with respect to temporal predictability. Specifically, participants were tasked with pressing a button using their left or right hand immediately in response to visual prompts (i.e., either an “L” or “R” on screen). ERPs to sound stimuli, which were elicited immediately in response to button presses, were corrected for motor activity through subtraction of those produced in an identical condition that did not involve sound stimuli. The same visual stimuli were used in a condition requiring participants to passively observe temporally-predictable sound. Visual cues were followed by a delay that was made equal to the mean reaction time of participants in the self-generation task (i.e., resulting in the same interval, on average, between the visual prompt and tone presentation). A third condition involved presentation of sound stimuli without accompanying visual cues, supporting examination of ERPs in response to tones that were not predictable in time. Sowman et al.

(2012) observed a similar reduction in N1 amplitude for both self-generated tones and externally-generated tones that were made predictable in time, relative to passively observed tones that were not temporally predictable. On this basis, they concluded that a significant portion of the suppressed neurophysiological response to self-generated stimuli is a result of their inherent temporal predictability.

In another recent investigation, Klaffehn et al. (2019) compared N1 components elicited by self- and externally-generated tones that were either unpredictable in time, or cued using a ‘loading bar’ visual stimulus (i.e., a bar that filled at a continuous rate over 750 ms to herald the onset of sound stimuli). The amplitude of auditory N1 components was found to be smaller in response to externally-generated tones that were made temporally predictable. Despite this, N1 amplitudes elicited by self-generated tones were found to be suppressed relative to those of externally-generated tones even when these were made predictable in time. On the basis of these results, it was concluded that temporal predictability alone is not sufficient to account for the suppression of self-generated sensations. However, these results further highlight the need to carefully control for the effects of temporal predictability in research examining sensory attenuation.

1.5.2 Temporal control

Another variable that may present a potential confound to studies of sensory attenuation is temporal control (i.e., the use of one’s actions to control the point in time at which a stimulus will occur). Because one must actively contribute to the generation of a stimulus in order influence its timing, externally-generated stimuli are not subject temporal control. In contrast, self-generated stimuli may be produced according to participants own timing or in response to cues that constrain the agent’s level of temporal control. Relatively few studies have attempted to account for differences in temporal control when comparing the neurophysiological response to self- and externally-generated stimuli. Despite this, there is some evidence to suggest that the magnitude of sensory response may be influenced by its effects. For example, Weiss et al. (2011) observed that the perceived loudness of sounds elicited by self-generated stimuli was less when these were generated in response to an experimenter's prompts than when self-paced. These findings may thereby reflect an amplification effect associated with temporal control, such that sensations are less attenuated under such conditions. Despite this, investigations into the sensory attenuation phenomenon have typically involved self-paced motor activity without regard for such influences (see Hughes et al., 2013b). Because the level of sensory attenuation may be underestimated in these circumstances, further research is needed to delineate the effects of temporal control from self-generation and the other factors influencing neurophysiological responses.

1.5.3 Non-motor identity prediction

Recent theories have proposed that prediction mechanisms facilitate the active construction of perceptual experience (Friston, 2005; Lee & Mumford, 2003). These frameworks propose that perception is founded on probabilistic inference and corrected based on the detection of discordant sensory information across hierarchies of perceptual representation (Clark, 2013; Friston, 2005; Mumford, 1992; Rao & Ballard, 1999). The influential theory of predictive coding was formalized by Friston (2005) to capture this notion, suggesting that the neural response elicited by stimuli reflects the level of mismatch between predicted and actual sensation. Fundamentally, this framework proposes that the neurophysiological response expected to result from a stimulus is inversely proportionate to the degree to which it may be predicted whether it is self- or externally-generated.

Several studies have provided evidence that the neurophysiological response to a stimulus is influenced by non-motor prediction (i.e., predictability regarding the nature of a stimulus based on the relationship between external events). In a study by Lange (2009), the amplitude of auditory N1 components that were elicited by tones with a pitch frequency made predictable by preceding sequences were found to be smaller than those following sequences that supported no such prediction. The phenomenon of repetition suppression may also provide evidence reflecting attenuation of the cortical response associated with non-motor identity prediction. Repetition suppression describes an observed reduction in neural response that is elicited by repeated stimuli (Desimone, 1996), and is among the most widely studied neurological phenomena (Auksztulewicz & Friston, 2016). While previous theories held that repetition suppression emerges as a result of neuronal fatigue (Grill-Spector et al., 2006) or refined engagement of neuronal populations (Wiggs & Martin, 1998), there is some evidence to suggest that the phenomenon emerges as a result of heightened predictability over successive exposures (Auksztulewicz & Friston, 2016; Mayrhauser et al., 2014; Summerfield et al., 2008). That is, as one becomes more familiar with the timing and nature of a repeating stimuli, increased predictability reduces the level of prediction error and therefore the observed neural response. These findings therefore reflect evidence in support of a reduced neurophysiological response to stimuli when the identity (i.e., pitch frequency in the case of sound) is made predictable.

By demonstrating that the cortical response to a stimulus is suppressed based on non-motor identity prediction, these findings highlight the importance of controlling for such factors in the investigation of sensory attenuation and theoretical frameworks to account for its effects. That is, the suppression of predictable self-generated sensations is not sufficient to demonstrate that these effects rely on predictions that are associated with a motor-command. An agent’s expectations regarding the outcome of their action (e.g., “movement of my finger to press this button will produce a sound”) must be differentiated from their predictions based on the relationship between external events (e.g., “if this button is pressed, a sound will be produced”). On this basis, it has been proposed that paradigms used to study sensory attenuation have left open the possibility that suppression of self-generated sensations may result from more generalised prediction in the absence of motor commands. Dogge et al. (2019), for example, have argued that there is limited evidence to support the direct involvement of motor-based prediction in the suppression of self-generated sensations involving environment-related outcomes (e.g., sound resulting from a button press). Instead, they argue that the observed effects may be facilitated by non-motor predictions. It is worth noting, however, that generalised prediction-based suppression has itself been subject to recent scrutiny. For example, a review of its effects in the visual system identified that robust evidence has been provided in only a subset of circumstances involving learned associations over multiple testing sessions (Feuerriegel et al., 2021). These results may therefore negate the influence of non-motor prediction in common experimental techniques used to study sensory attenuation, including the press-listen paradigm. Nevertheless, further research is necessary to disentangle effects involving generalised prediction from those associated with motor commands within the IFM framework.

1.5.4 Attention

In addition to the properties of an eliciting stimulus, one's cortical response is influenced by internal factors such as the allocation of attention. Broadly, attentional effects have been observed with regard to the task relevance of sensory material (i.e., attention to a subset of stimuli based on sensory modality, stimulus properties or specific receptor fields) and their timing (i.e., attention based on orienting to a given moment). With regard to effects involving the relevance of sensory material to the auditory evoked potential, selective N1 *enhancement* has been observed in response to specific tone frequencies when their observation is required by the demands of a task (e.g., keeping tally of high pitch tones in a sequence involving several tone frequencies; Kauramäki et al., 2012; Kauramäki et al., 2007; Okamoto et al., 2007). Similarly, Hillyard et al. (1973) demonstrated that sounds presented to an ear that is subject to participant attention elicit larger N1 amplitudes than those directed to an ear for which stimuli are not task relevant. With regard to temporal orienting, anticipation of auditory stimuli at a given moment in time has been shown to be another factor that can heighten selective attention and corresponding response within primary sensory cortices (see Lange, 2013). In an experiment by Lange et al. (2003), for example, the auditory N1 to sounds elicited at attended moments were found to be larger than for identical stimuli presented at unattended moments, when other factors were controlled. Overall, these findings demonstrate that larger N1 amplitudes are elicited by sound that is more highly attended.

Given significant attention-related effects on primary cortical response, research has highlighted the potential confound these present to studies of sensory attenuation (see Horváth, 2015). In particular, it has been proposed that the attenuation of self-generated sensation may result from differences in the distribution of attention between processes involved in the production of movement and processing of resultant stimuli. In an experiment aimed at exploring this possibility, Saupe et al. (2013) compared the response to self-generated tones and those produced externally in tasks that required them to discriminate trials based on the interval between each stimulus presentation. Although an attention-related effect was observed, such that conditions involving heightened attention to sound stimuli exhibited larger N1 amplitudes, these were not found to be sufficient to fully account for sensory attenuation effects. Similarly, Timm et al. (2013) manipulated the task relevance of stimulus features by asking participants to count button-presses, tones or visual stimuli. Results of their investigation suggested that topographical effects associated with the manipulation of attention (i.e., changes in electrical potential across participants' scalps, as indicated by EEG) differed from those reflecting the suppression of self-generated sensations. While acknowledging that attention may play a role in sensory attenuation, Timm et al. (2013) conclude that these findings implicate additional factors, such as motor-based prediction. Despite indications that sensory attenuation may not be fully attributable to the effects of attention, it remains an important consideration in research aimed at exploring the phenomenon.

1.6 Sensorimotor integration and agency

In addition to influencing sensory processing of self-generated stimuli, action-effect predictions are believed to facilitate the *generation* of movement. Ideomotor theory (James, 1890), which remains influential in the motor literature (see review by Shin et al., 2010), proposes that action is initiated through the internal activation its predicted sensory effects. Through its capacity to integrate action and perception within a shared representational system, it has been proposed that the IFM may facilitate the selection of motor commands as well as the processing of resultant stimuli (Hommel et al., 2001; Prinz, 1990; Prinz, 1997; Wolpert et al., 1995). In this way, the IFM may support the selection and initiation of a motor action based on its anticipated outcomes, then facilitate a response based on observed discrepancies in the observed outcome. It has also been postulated that this system gives rise to our conscious awareness of action, based on predictions derived from efferent commands rather than proprioceptive feedback per se (Blakemore et al., 2002; Wolpert & Ghahramani, 2000). This notion is supported by the phantom limb phenomenon, in which voluntary movement of an amputated limb may still be perceived, as well as the adaptation of this perception through visual feedback (Ramachandran & Rogers-Ramachandran, 1996).

Because the selection of motor commands are based on an agent’s expectations regarding their capacity to achieve intended outcomes (see Balleine & Dickinson, 1998), one’s sense of agency is believed to also relate to the alignment of predicted and actual sensory experience (see Haggard, 2017). Evidence for this relationship has been provided by research into the phenomenon of intentional binding, whereby a reduction is observed in the perceived interval between deliberate action and stimuli presented following a brief delay (Haggard et al., 2002). Significantly, intentional binding was found by Haggard et al. (2002)

to involve change in the perceived timing of both action and the resulting stimulus. While action is experienced as having occurred later in time, resulting stimuli are experienced as having occurred earlier. Moore and Haggard (2008) found that, for motor action that does not consistently result in the presentation of a stimulus, change in the perceived timing of action is larger when stimuli are subsequently presented than when they are not. This suggests that intentional binding may retrospectively affect the perceived timing of action, based on resulting sensations. Moore and Haggard (2008) also found that change in the perceived timing of action is larger when the perceived likelihood of a resulting stimulus was higher (i.e., based on prior expectations). Intentional binding thereby appears to be influenced by both prospective and retrospective factors, which contribute to one's sense of agency through the prediction of action-effects and their observation respectively.

The notion that action-effect predictions guide movement is also a central tenet to the theory of active inference (Friston et al., 2009). This account builds on the influential free-energy principle (Friston, 2005; see also Rao & Ballard, 1999), which proposes that our perceptual system operates to minimise the energy consumed by prediction errors that are created when anticipated and actual sensations deviate. Such error may be reduced with an improvement in the accuracy of predictions, or by movement that elicits anticipated sensations (Friston, 2009; Friston et al., 2010). The proposed operation of IFMs and active inference theory thereby postulate complementary but distinct mechanisms by which action-effect predictions contribute to the generation and coordination of movement.

Pickering and Clark (2014) contrast two accounts of internal forward models that differ in the degree to which efference copies are treated as integral or auxiliary components of the motor system. The auxiliary account reflects a traditional view of efference copies, contending that they operate in parallel to motor circuitry and allow prediction of the sensations that result from self-generated action (Franklin & Wolpert, 2011; Kawato, 1999;

Wolpert & Kawato, 1998). This model contends that predictive mechanisms are initiated in the motor cortex as copies of command signals, but diverge from motor circuitry before these reach the motor plant (i.e., the unit implementing motor action; Pickering & Clark, 2014). In contrast, the integral forward model that has emerged from predictive coding theory emphasises the integration of these systems (Clark, 2013; Friston, 2011; Herwig, 2015), such that descending predictions extend down to encompass the motor responses themselves (Friston et al., 2010). According to this, corollary discharge (i.e., the anticipated sensory consequences of motor activity) serves to initiate movement by providing a template for action (Friston et al., 2010). Cascading prediction errors, generated through mismatch between the template and proprioceptive sensation, are believed to be corrected through corticospinal reflex arcs that bring about the desired movement (Friston, 2011; Mathys et al., 2011).

Kilner et al. (2007) theorise that the integration of motor plants within an internal forward model also allows the system to infer motor commands of an observed agent. That is, the generative model may be inverted to determine the causes of sensory information by reflecting observed behaviour in a manner typically associated with the operation of mirror neurons (Kilner et al., 2007). If true, predictive systems involved in attenuating the neurological response to one’s own actions convey predictions regarding exteroceptive sensations (i.e., those resulting from the activity of external agents) as well. This notion further challenges the tenet that sensory attenuation corresponds directly to one’s agency regarding the outcome of action. Instead, it has been proposed that the distinction between predicted sensations resulting from self-generated and external action is encoded within the relative weighting of prediction errors and therefore the *level* of observed suppression (Kilner et al., 2007; Mathys et al., 2011).

1.7 Distinguishing volitional and stimulus-driven movement

Different forms of action are accompanied by varying levels of conscious intent and volition. While certain actions are initiated in the absence of external sensory cues, these may be distinguished from forms of movement that are involuntary; whether because they are enacted instinctively in response to external cues (e.g., simple reflexes) or are otherwise without conscious intent (e.g., highly automatized behaviours, tics, and tremors; Fried et al., 2017). Differences in the neural mechanisms responsible for initiating, monitoring outcomes and adjusting each form of movement may have relevance to models of sensorimotor integration.

An informative distinction has been made between motor actions involving ideomotor (i.e., action-effect) and sensorimotor (i.e., stimulus-response) associations (e.g., Neumann, 1984). Specifically, action-effect associations may be used to identify motor activity to achieve desired outcomes in a manner consistent with mechanisms proposed by ideomotor theory. In contrast, stimulus-response associations may give rise to motor action in response to external cues with less regard for their sensory consequences. A contrast between these forms of action is supported by evidence that identical overt actions may be guided by either form of learned association, depending on whether the action is volitional (i.e., internally-cued) or stimulus-driven (i.e., externally-cued; Herwig et al., 2007). Importantly, several studies have yielded evidence that the ideomotor principle (i.e., that action is guided by internal activation of its anticipated consequences) may be more influential with regard to intention-based action (Herwig et al., 2007; Pfister et al., 2011). In contrast, stimulus-driven action has been described as a form of ‘prepared reflex’ (Hommel, 2000), with control for the action relinquished to an activating stimulus.

Distinct mechanisms contributing to volitional and stimulus-driven action are supported by research demonstrating that these action are associated with different neuroanatomical structures (see Fried et al., 2017). Effects involving the supplementary motor area (SMA) and pre-SMA are particularly instructive, given that these regions have been found to be involved to a larger degree in the generation of volitional action than stimulus-driven movement (Debaere et al., 2003; Fried et al., 2011). Significantly, an “urge to move” has been reported in response to stimulation of the SMA and pre-SMA (Desmurget et al., 2009; Fried et al., 1991). Stimulation with higher levels of current to either the SMA or primary motor cortex has been found to elicit overt movement, though patients have not reported an “urge to move” with regard to the latter (Fried et al., 2017; Fried et al., 1991; Haggard, 2011). In this way, differing neuroanatomical substrates to volitional and stimulus-driven movement support a distinction between these forms of action that is potentially informative to understanding perceptions of agency in each.

1.8 Clinical implications of dysfunction in corollary discharge

Schizophrenia has long been associated with difficulties in source monitoring, which are believed to contribute to symptoms involving the misattribution of self- and externally-generated events (Feinberg, 1978; Frith, 1992; Vinogradov et al., 1997). Several examples are evident within the proposed ‘first-rank symptoms’ of schizophrenia (Frith et al., 2000a), which identify a series of (arguably) pathognomonic experiences associated with the condition (i.e., those that are most characteristic and distinct; Carpenter et al., 1973; Mellor, 1970; Schneider, 1959). This includes the ‘thought echo’ hallucination, whereby a person with schizophrenia may experience repetition of their own thoughts by a voice that is perceived to be that of another agent. It has been proposed that this phenomenon represents a misattribution of one’s own internal monologue to an external agent (Frith, 1992). Similarly, the misattribution of one’s own movements to another party may give rise to ‘delusions of control’ (Frith et al., 2000a). Someone experiencing this form of delusion perceive that their own motor actions have been caused by an external person or other force (e.g., "The force moved my lips. I began to speak. The words were made for me."; Frith, 1992; p. 171). These examples serve to demonstrate that errors in source monitoring, involving confusion between self- and externally-generated sensations, are common symptoms of schizophrenia. To the degree that these errors are common in schizophrenia and uncommon in other disorders, delineating the mechanisms that give rise to these symptoms is important to understanding the aetiology of the condition.

Given its role in supporting one's perception of agency over self-generated sensations, dysfunction of corollary discharge mechanisms have been proposed to explain irregularities in the attribution of self- and externally-generated sensations in schizophrenia (Feinberg & Guazzelli, 1999). This notion has been supported by evidence indicating that people with schizophrenia exhibit deficits in sensory attenuation, reflecting a failure to distinguish and suppress self-generated sensations. In particular, Blakemore et al. (2000) compared ticklishness ratings of self- and externally-generated tactile sensations in patients with schizophrenia/schizoaffective disorder and healthy controls. While healthy controls and patients not exhibiting select first-rank symptoms (i.e., auditory hallucinations or passivity symptoms) were found to rate self-generated sensations as less ticklish than those produced by the experimenter, patients exhibiting these first-rank symptoms did not. Electrophysiological studies have provided additional evidence that symptoms of schizophrenia may involve dysfunction in corollary discharge mechanisms. In particular, research has consistently demonstrated reduced levels of sensory attenuation as reflected within N1 component amplitudes in both talk-listen and press-listen paradigms (e.g., Ford & Mathalon, 2012; Ford, Mathalon, Kalba, et al., 2001; Ford et al., 2014; Heinks-Maldonado et al., 2007; Whitford et al., 2011). Taken together, these studies suggest that dysfunction in processes contributing to sensory attenuation may contribute to irregularities in the attribution agency in people schizophrenia. In this way, an improved understanding of the mechanisms underlying sensory attenuation may serve to advance knowledge and therefore treatment approaches for people living with the condition.

1.9 Aims and scope

The overarching aim of the present body of work was to investigate processes involved in the IFM, including factors affecting the production and processing of self-generated stimuli compared with those produced externally. This was achieved across four separate investigations, presented in subsequent chapters. A dynamic approach was taken, such that each investigation sought to extend on relevant findings from those prior.

In the first investigation (Chapter 2), effects of temporal predictability and temporal control were examined with regard to their potential contribution to the sensory attenuation phenomenon. We utilised a novel paradigm that involved a ‘ticker-tape’ style presentation to support cueing of action and temporal predictability regarding the onset of externally-generated stimuli. Comparison conditions involved tones elicited by uncued (i.e., self-paced) action and externally-generated tones that were not predictable in time (i.e., not accompanied by informative visual cues). A key finding of this study was that temporal control amplifies N1 amplitude in a manner that countervails the sensory attenuation phenomenon.

A second investigation (Chapter 3) aimed to explore the role of action-effect contingency (i.e., the likelihood of action eliciting a stimulus) in observed suppression of N1 amplitude for stimuli resulting from cued (i.e., stimulus-driven) versus uncued (i.e., volitional) action. We sought also to explore differences in pre-stimulus indices of motor preparation for each form of action, as well as novel effects that appear to reflect the termination of motor-related attention and suppression of attentional capture by resultant stimuli.

In the third investigation (Chapter 4), we aimed to contrast effects of stimulus predictability on the primary cortical responses to self- and externally-generated stimuli in a manner that also controlled for the effects of temporal predictability. We sought to differentiate sensorimotor processes in stimulus-driven and volitional action, including analyses of components associated with attention and error monitoring. Despite strong power and significant differences in the amplitudes of other ERP components, this study failed to replicate amplification of N1 amplitude for stimuli resulting from volitional versus stimulus-driven action.

A fourth investigation (Chapter 5) was motivated by this failure to replicate, which we hypothesised was due to longer inter-trial intervals (ITIs) following the introduction of a prompt that asked participants to slow down when trials were produced in close succession. To assess this possibility, we conducted additional analyses of an experiment in the first investigation, which implemented a median split based on ITI by condition and participant. An exploratory analysis was also undertaken to assess potential differences in sensory gating between the conditions, given the relevance this may have to sensorimotor effects associated with the IFM.

In a general discussion, I integrate overall findings with the broader literature and make recommendations for future research. Implications are discussed with respect to the effects of temporal predictability and control, as well as those relating to attention, non-motor identity prediction and agency. On the basis of these normative results, we propose tentative consequences for understanding apparent dysfunction in corollary discharge mechanisms among people with schizophrenia and new avenues for exploration.

2. Sensory attenuation is modulated by the contrasting effects of predictability and control

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2.1 Abstract

Self-generated stimuli have been found to elicit a reduced sensory response compared with externally-generated stimuli. However, much of the literature has not adequately controlled for differences in the temporal predictability and temporal control of stimuli. In two experiments, we compared the N1 (and P2) components of the auditory-evoked potential to self- and externally-generated tones that differed with respect to these two factors. In Experiment 1 (*n* = 42), we found that increasing temporal predictability reduced N1 amplitude in a manner that may often account for the observed reduction in sensory response to self-generated sounds. We also observed that reducing temporal control over the tones resulted in a reduction in N1 amplitude. The contrasting effects of temporal predictability and temporal control on N1 amplitude meant that sensory attenuation prevailed when controlling for each. Experiment 2 (*n* = 38) explored the potential effect of selective attention on the results of Experiment 1 by modifying task requirements such that similar levels of attention were allocated to the visual stimuli across conditions. The results of Experiment 2 replicated those of Experiment 1, and suggested that the observed effects of temporal control and sensory attenuation were not driven by differences in attention. Given that self- and externally-generated sensations commonly differ with respect to both temporal predictability

and temporal control, findings of the present study may necessitate a re-evaluation of the experimental paradigms used to study sensory attenuation.

2.2 Introduction

The term 'sensory attenuation' has been used to describe a reduction in the neurophysiological response and subjective intensity of sensations elicited by self-generated stimuli, as compared to that of physically identical stimuli when externally-generated (e.g., Blakemore et al., 1998; Schafer & Marcus, 1973). This phenomenon has been argued to involve the operation of internal forward models (Miall & Wolpert, 1996), in which duplicates of the motor commands ('efference copies') are used to predict and suppress the sensory consequences of action (Ford & Mathalon, 2012). In this way, sensory attenuation is believed to occur when one's predictions regarding the outcome of an action match the actual sensory feedback (Wolpert, 1997). Research has explored the effects of sensory attenuation across a variety of action types and sensory modalities, including visual continuity during saccadic eye movements (Bridgeman, 1995; Thakkar et al., 2015), suppression of self-generated speech (Houde et al., 2002; Whitford, 2019) and the inability to tickle oneself (Blakemore et al., 1998). Research has also observed sensory attenuation based on less innate action-stimulus pairs, including computer-generated tones triggered by a button press (Aliu et al., 2009; Klaffehn et al., 2019; Lange, 2011; Martikainen et al., 2005; Sato, 2008; Sowman et al., 2012). However, despite an extensive corpus of research investigating its mechanisms (see Horváth, 2015), there are at least two potential methodological confounds that draw into question the existence and magnitude of the sensory attenuation effect (Hughes et al., 2013b). In particular, much of the sensory attenuation literature has inadequately controlled for the effects of temporal predictability and temporal control.

Temporal predictability – the ability to predict the onset of a stimulus – is intrinsic to many self-generated sensations, which often arise more-or-less instantaneously from one's own motor actions. Externally-generated stimuli may also be made temporally predictable by providing cues to indicate their impending onset. Research has demonstrated that increasing the temporal predictability of an externally-generated stimulus reduces both its subjective intensity and neurophysiological response (Lange, 2009; Schafer & Marcus, 1973; Schwartze et al., 2011; Sowman et al., 2012; Weiskrantz et al., 1971). Although sensory attenuation has been found to be robust to reductions in the temporal predictability of self-generated sensations (Bäß et al., 2008), evidence suggests that it is reduced with increasing action-stimulus asynchrony (Horváth et al., 2012; Pinheiro et al., 2019). Despite evidence regarding the effects of temporal predictability, however, sensory attenuation has often been studied by comparing externally-generated stimuli that are unpredictable in time with those elicited immediately in response to one's actions. While some studies have attempted to control for this effect in their design, by supporting prediction regarding the onset of externally-generated stimuli (e.g., making these periodic; Aliu et al., 2009; or visually cued; Lange, 2011), much of the research investigating sensory attenuation has not (Hughes et al., 2013b). Of the research that has controlled for temporal predictability, several studies have observed that the magnitude of sensory attenuation is reduced when accounting for its effects (Schafer & Marcus, 1973; Sowman et al., 2012; Weiskrantz et al., 1971). These findings highlight the importance of controlling for temporal predictability in sensory attenuation research.

Temporal control – use of one's actions to control the point in time at which a stimulus will occur – is another potential confound in studies of sensory attenuation. To exert temporal control over a stimulus, one must have actively contributed in some manner to its generation. In comparison, individuals lack temporal control over externally-generated stimuli. There is some evidence to suggest that temporal control may influence the magnitude of one's sensory response. For example, Weiss et al. (2011) observed that the subjective intensity of self-generated stimuli was less when generated in response to an experimenter's prompts than when elicited according to participants' own timing. Despite this, sensory attenuation studies have typically involving self-paced motor action based on limited guidance with respect to timing (Hughes et al., 2013b). The effect of temporal control on sensory response to self-generated stimuli is therefore yet to be systematically investigated in the sensory attenuation literature.

The present investigation aimed to delineate the influence of temporal predictability and temporal control in the phenomenon of sensory attenuation. Specifically, two experiments investigated the effects of temporal control and temporal predictability on the N1 component of the auditory evoked potential. The N1 is a large negative component that is commonly investigated in psychophysiological studies of sensory attenuation (e.g., Ford, Gray, et al., 2007; Heinks-Maldonado et al., 2005; Lange, 2011; Oestreich et al., 2015, 2016; Whitford et al., 2017). It has a frontocentral topography that peaks 75 to 125 ms after stimulus onset and at least three subcomponents that are believed to originate in the supratemporal plane, superior temporal gyrus, and regions within the motor cortex and/or cingulate gyrus (see Giard et al., 1994; Näätänen & Picton, 1987). The N1 component is commonly examined in studies of acoustic perception, as it provides a reliable indicator of neurophysiological response within the primary auditory cortex (Zouridakis et al., 1998). Importantly, the amplitude of the N1 has been shown to be intensity-dependent (i.e., louder sounds elicit larger N1 amplitudes when all else is held equal; Mulert et al., 2005). An implication is that if the N1 is found to be smaller in response to self-generated sounds compared to passively-generated sounds, this suggests that the brain represents these stimuli as being less intense (Whitford, 2019).

2.3 Experiment 1

In Experiment 1, we first tested the hypothesis that N1 amplitude would be reduced when externally-generated sound stimuli were made temporally predictable. Such an effect may thereby partly account for apparent sensory attenuation (i.e., reduced N1 amplitude to self-generated sounds) when differences in temporal predictability between self- and externally generated sensations have not been adequately controlled. In addition, we hypothesised that further amplitude reductions would be observed in conditions that required participants to generate tones according to precise external cues (i.e., when their temporal control over the sounds was constrained) and anticipated larger N1 amplitudes when participants were asked to generate tones in a self-paced manner (i.e., while exerting temporal control). This hypothesis was based on the reduction in subjective intensity of sensation that Weiss et al. (2011) observed when the timing of self-generated stimuli was based on prompts provided by the experimenter, compared to when these were self-paced.

2.3.1 Method

2.3.1.1 Participants

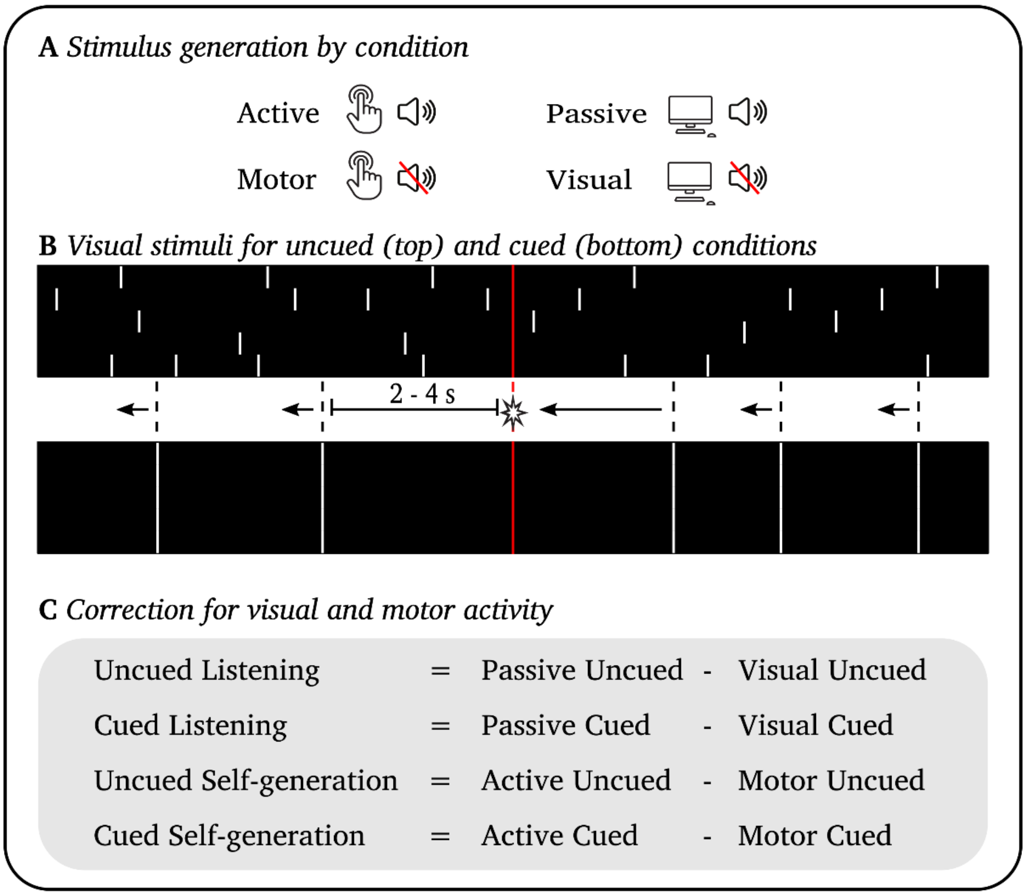
The final sample consisted of 42 healthy participants (25 females), aged between 17 and 33 years (*M* = 20.69, *Mdn* = 19.24, *SD* = 3.71). Data from an additional participant was found to have an insufficient number of valid segments following artefact rejection, based on a minimum threshold of 30 usable trials per condition (see *EEG Processing and Analysis*), and was excluded from further analysis. Participants were recruited through the University of New South Wales (UNSW) electronic participants recruitment system (SONA-1) and received course credit in exchange for their participation. The study was approved by the UNSW Human Research Ethics Advisory Panel (Psychology).

2.3.1.2 Materials and design

Participants were seated facing a BenQ XL2420T computer monitor (24-inch, 1920 × 1080 resolution screen) at a distance of approximately 60 cm. They were fitted with Sennheiser HD201 headphones and an EEG recording cap, containing a BioSemi ActiveTwo system on which 64 Ag/AgCl active electrodes were positioned according to the extended 10–20 system. Recordings from an electrode placed below the left eye was used in conjunction with Fp1 to develop a vertical electro-oculogram (EOG), and a horizontal EOG was constructed using electrodes placed adjacent to the outer canthus of each eye. Electrodes were also placed on the left and right mastoids, as well as the tip of the nose. The CMS and DRL electrode sites were used as ground electrodes during data acquisition, which was conducted at a sampling rate of 2048 Hz.

In each experimental block, participants watched a visual animation. Against a black background, a red (fixation) line was positioned at the centre of the screen. This vertical line was one pixel wide and approximately six centimetres in length (i.e., 5.4 degrees of visual angle). Participants were instructed to fix their gaze on the centre of this line for each of the eight experimental conditions. In four *uncued* conditions (i.e., *active, motor, passive* and *visual*), a randomly spaced sequence of white line fragments appeared from offscreen on the right of the monitor and moved leftward across the screen at a constant velocity of 3°/s (see Fig. 2.1B). These fragments were equal in length and distributed in five adjacent rows spanning the height of the fixation line. After crossing behind the fixation line, the white line fragments continued leftward off the screen. In the *active uncued* and *motor uncued* conditions, participants were asked to repeatedly press a keyboard button, at will. They were asked to aim for an interval of approximately two to four seconds between each button-press and to make their timing “as random and unpredictable as possible”. In the *active uncued* condition, each button press elicited an 85 dB SPL (A-weighted) pure tone (1000 Hz, 10 ms ramp, 100 ms duration), delivered via headphones. For low-latency delivery of auditory stimuli, these were delivered via an AudioFile Stimulus Processor (Cambridge Research Systems). In the *passive uncued* and *visual uncued* conditions, participants were not instructed to press any keys but to remain focussed on the fixation line while stimuli were presented to them. Identical tones were delivered in the *passive uncued* condition based on inter-stimulus intervals (ISIs) established during the *active uncued* condition, which was always presented first in each block. Participants were presented with silent audio tracks in the *visual uncued* and *motor uncued* conditions, with the ISIs based on the *active uncued* condition.

Fig. 2.1. Experiment 1 visual stimuli and schematic



Uncued Listening = Passive Uncued - Visual Uncued
Cued Listening = Passive Cued - Visual Cued
Uncued Self-generation = Active Uncued - Motor Uncued
Cued Self-generation = Active Cued - Motor Cued

A. Participants pressed a keyboard button to initiate events in the *active* and *motor* conditions, while these were externally-generated (by computer) in the *passive* and *visual* conditions. Events involved an 85 dB tone (1000 Hz) in the *active* and *passive* conditions, while a silent audio track was presented in the *motor* and *visual* condition. **B.** In four *uncued* conditions, including one for each of the *active, passive, motor* and *visual* event variants, line fragments moved from right to left at a constant rate and were randomly distributed with a density that corresponded to five fragments (i.e., one per row) every three seconds. In the *active uncued* condition, participants were instructed to press a keyboard button approximately every two to four seconds at will. Each button press elicited a 1000 Hz tone of 85 dB, delivered via participant headphones. The *motor uncued* condition was identical, except that button presses did not elicit tones. In the *passive uncued* condition, participants were instructed to simply observe as identical (computer-triggered) tones and visual stimuli were presented. Although they were not informed, the timing of these tones was based on the participant’s own button presses during the preceding *active uncued* condition. In the *visual uncued* condition, participants were asked to simply watch the uncued animation while silent audio tracks were presented based on participants’ timing in the preceding *active uncued* block. In four *cued* conditions, including one for each of the *active, passive, motor* and *visual* event variants, longer white lines moved from right to left at a constant rate and were spaced according to the timing established by participants in the preceding *active uncued* condition. In the *active cued* and *motor cued* conditions, participants were asked to press the keyboard button at the precise moment that each passing line intersected with the fixation line. Button presses resulted in a tone in the *active cued* condition, while these were absent in the *motor cued* condition. Participants were instructed to simply watch the visual animation in both the *passive cued* and *visual cued* conditions. Computer-triggered tones were presented at the precise moment that each passing line intersected with the fixation line in the *passive cued* condition, while silent audio tracks were presented in the *visual cued* condition. **C.** The eight experimental conditions supported development of four analysis conditions: *uncued listening, cued listening, uncued self-generation* and *cued self-generation*, where *listening* conditions represent visual-corrected *passive* conditions and *self-generation* conditions represent motor-corrected *active* conditions.

In the four *cued* conditions (i.e., *action cued, motor cued, passive cued* and *visual cued*), vertical white lines with equal length and width to the fixation line appeared from offscreen to the right of the monitor and moved leftward across the screen at a constant rate (see Fig. 2.1B). These lines were also spaced according to the timing established by participants through their button presses in the *active uncued* condition. In the *active cued* and *motor cued* conditions participants were instructed to press a key at the precise moment that each stimulus line intersected with the fixation line. A tone was delivered each time the key was pressed in the *active cued* condition, while silent audio tracks were presented in the *motor cued* condition. Participants were not asked to press the keyboard button in the *passive cued* or *visual cued* conditions. In the *passive cued* condition, a tone was presented each time a vertical white line passed the fixation line, while participants were presented with silent audio tracks in the *visual cued* condition. Audio tracks for the *passive* and *visual* conditions were also delivered via the AudioFile Stimulus Processor.

Trials were divided into sets of eight blocks, with 30 trials per block. Participants underwent three sets, meaning that there were 90 trials of each of the eight conditions in total. Each set commenced with an *active uncued* block, followed by one block of each other condition presented in random order. Data collection lasted approximately 50 min, and included short breaks between blocks.

The auditory evoked potentials for each condition were corrected by subtracting the ERPs for tasks that did not involve auditory stimuli but were otherwise identical. These *visual* and *motor* conditions were used to correct auditory evoked potentials of the *passive* and *active* conditions, respectively. There were thus eight block types in total: *uncued* and *cued* condition variants of *passive, active, visual,* and *motor*. These eight experimental conditions supported development of four analysis conditions: *uncued listening, cued listening, uncued self-generation* and *cued self-generation,* where *listening* conditions represented visual-corrected *passive* conditions and *self-generation* conditions represented motor-corrected *active* conditions (see Fig. 2.1C).

The corrected waveforms allow comparison of self- and externally-generated tones in a manner that accounted for both temporal predictability and temporal control (see Table 2.1). Four contrasts hold particular relevance. Firstly, comparison of *uncued listening* and *cued listening* allowed evaluation of the effects of *temporal predictability*. Secondly, the effect of *temporal control* could be assessed through comparison of *cued self-generation* and *uncued self-generation*. Thirdly, the *classic sensory attenuation* effect (i.e., without controlling for the effects of temporal predictability or temporal control) was demonstrated through comparison of *uncued listening* and *uncued self-generation.* Finally, the *sensory attenuation (controlled)* effect (i.e., controlling for both temporal predictability and temporal control) was evaluated based on comparison of *cued listening* and *cued self-generation*.

Table 2.1

Analysis Condition Characteristics and their Contrasts

	Self-generated	Temporal Predictability	Temporal Control	Contrasts		
				Uncued listening	Cued listening	Uncued self-generation
Uncued listening						
Cued listening		✓		TP		
Uncued self-generation	✓	✓	✓	SG, TP, TC	SG, TC	
Cued self-generation	✓	✓		SG, TP	SG	(TC)

Note. Contrasts represent the characteristics of row conditions relative to those in columns. SG = self-generation, TP = temporal predictability and TC = temporal control. Brackets denote relative absence of characteristic in row condition.

2.3.1.3 EEG processing and analysis

Data were referenced to the nose electrode and filtered offline using BrainVision Analyzer. A notch filter (50 Hz) was applied, as well as a phase-shift free half-amplitude Butterworth band-pass filter (0.1 Hz to 30 Hz) with 48 dB/Oct slope. Data were then segmented into 600 ms epochs, which included 200 ms prior to sound stimulus presentation and 400 ms post-onset. Eye movement artefacts were corrected using the method described by Miller et al. (1988), based on the approach developed by Gratton et al. (1983). Segments found to contain peak-to-peak amplitudes in excess of 200 µV were excluded. Baseline correction was applied using the average voltage in the 200 ms prior to stimulus onset.

The primary dependent variable was the amplitude of the auditory N1 component, while the P2 was a secondary component of interest. The N1 component of the auditory event-related potentials (ERPs) was analysed using pooled recordings taken at electrode sites Fz, FCz, and Cz, reflecting its frontocentral topography. The P2 component is known to have a more central distribution, and was therefore analysed using recordings taken at FCz, Cz and CPz. These were locked to auditory stimulus onset in the *passive* and *active* conditions. In the *motor* and *visual* conditions, segments were time-locked to the onset of each silent audio track. These conditions differed from the *active* and *passive* conditions only in that the audio track was silent, thereby supporting correction for the effects of motor action and visual animation respectively. Specifically, the *active* conditions were corrected by subtracting the ERPs of corresponding motor condition (i.e., *cued* and *uncued*), while the passive conditions were corrected by subtracting the ERPs of the corresponding visual condition.

Grand average waveforms were calculated based on at least 30 usable trials for each of the eight conditions. A one-way repeated measures ANOVA was used to assess potential differences in the number of trials included in grand average waveforms between conditions. This included trial counts for *active uncued* (*M* = 87.64, *SD* = 3.46), *active cued* (*M* = 87.62, *SD* = 4.10), *motor uncued* (*M* = 87.31, *SD* = 4.64), *motor cued* (*M* = 85.55, *SD* = 9.37), *passive uncued* (*M* = 86.40, *SD* = 6.43), *passive cued* (*M* = 86.10, *SD* = 8.28), *visual uncued* (*M* = 84.12, SD = 11.62) and *visual cued* (*M* = 84.60, *SD* = 9.91). Non-sphericity was identified by Mauchly's test (Mauchly, 1940) and corrected using the Greenhouse-Geisser method (Geisser & Greenhouse, 1958). Results did not reveal a statistically significant difference in the number of trials between conditions, $F(3.63, 148.72) = 2.196$, $p = 0.079$, partial $\eta^2 = 0.051$, $BF_{10} = 0.45$.

The N1 is known to have a frontocentral maximum (Zouridakis et al., 1998), which was consistent with observations in the present data (maximal at FCz). A more central P2 (maximal at Cz) was also consistent with expectations based on previous research (Potts et al., 1998). Analyses of the N1 component were based on pooled recordings at electrode sites Fz, FCz and Cz, as has been done previously in recognition of the maximal N1 signal at these locations (Jack et al., 2019; Näätänen & Picton, 1987; Whitford et al., 2017; Woods, 1995). Similarly, P2 component amplitudes were based on pooled recording at electrode sites FCz, Cz and CPz. Both N1 and P2 components were identified based on a collapsed localizer waveform (i.e., averaging across all participants and conditions; Luck & Gaspelin, 2017). The N1 component was identified as the most negative local minimum between 25 ms and 175 ms in the collapsed localizer waveform, which was identified at 97 ms post-stimulus. Mean amplitudes were calculated for each condition based on 20 ms windows centred on this peak (i.e., between 87 and 107 ms post-stimulus). The P2 component was identified as the most positive local maximum between 110 ms and 200 ms, which was found to occur at 175 ms in the collapsed localizer waveform. The mean amplitude of P2 components were consequently calculated based on sampled voltage between 165 ms and 185 ms.

2.3.1.4 Statistical analysis

One-way repeated measures analyses of variance (ANOVAs) were undertaken to assess the statistical significance of differences between component voltages observed in each condition. This statistical approach was selected on the basis that although the experimental design involved two factors (i.e., active/passive and cued/uncued), change between levels in one factor did not equate to the same conceptual change between levels in the other. For example, cues in the *passive* and *visual* conditions supported temporal predictability of stimuli while those in the *active* and *motor* conditions affected only temporal control (see Table 2.1). A 2 × 2 factorial ANOVA would therefore have risked conflating these effects. The Greenhouse-Geisser method (Geisser & Greenhouse, 1958) was used to correct for non-sphericity where this was identified by Mauchly’s tests (Mauchly, 1940).

A series of paired samples Student’s t-tests were conducted to evaluate differences between the mean voltage observed for components of each condition. The Benjamini-Hochberg method (Benjamini & Hochberg, 1995) was used to correct *p*-values so as to control the False Discovery Rate (FDR). Contrasts were only interpreted (i.e., using uncorrected *p*-values) when these remained significant following correction for multiple comparisons (i.e., $p_{corr} < 0.05$; see Appendix 1, Table A1.1). Where correction resulted in a contrast falling outside the critical *p*-value, this was explicitly acknowledged. Corrections were applied to control FDR by experiment (i.e., 12 contrasts in Experiment 1 and 30 contrasts in Experiment 2, see below). A Bayes factor (BF_{10}) was also developed for omnibus repeated measures ANOVAs, as well as each contrast. These comparisons included Cauchy priors with an r-scale of $1/\sqrt{2}$ for effect size (see Morey & Rouder, 2018), which have been recommended across a range of Bayesian statistical procedures, including regression (Gelman et al., 2008) and point null hypothesis testing (Jeffreys, 1998).

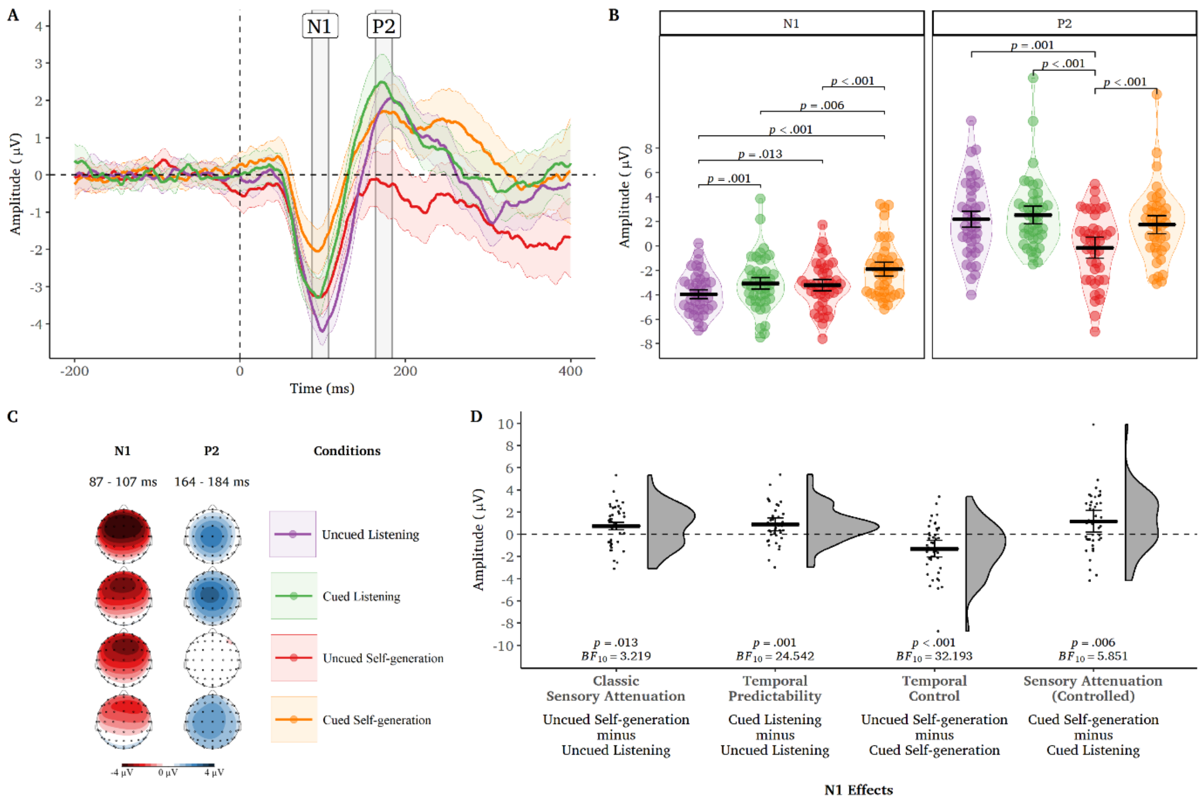
The accuracy of button presses in the *active cued* and *motor cued* conditions were compared using a paired samples Student's *t*-test. Inter-stimulus intervals (ISIs) were also analysed to confirm effective and consistent manipulation of timing in conditions involving participant input. Paired samples Student's t-tests were used to compare mean ISIs in *active uncued* and *active cued*, as well as the motor-only conditions used for their correction (i.e., *motor uncued* and *motor cued)*. Results from analyses of ISIs are provided in Appendix 1.

2.3.2 Results

2.3.2.1 N1

A one-way repeated measures ANOVA was conducted to assess differences in N1 amplitude (i.e., between 87 and 107 ms post-stimulus). Results revealed a statistically significant difference between conditions, $F(2.51, 103.01) = 13.171$, $p < 0.001$, partial $\eta^2 = 0.243$, $BF_{10} = 91{,}358.45$. A series of paired samples Student's t-tests were conducted to compare participants' mean N1 amplitudes across conditions. Results revealed that N1 amplitudes (µV) in the *uncued listening* condition ($M = -3.96$, $SD = 1.78$) were significantly more negative than those in each of the other conditions, including *cued listening* ($M = -3.07$, $SD = 2.24$), $t(41) = -3.46$, $p = 0.001$, $d = 0.44$, $BF_{10} = 24.54$, *uncued self-generation* ($M = -3.22$, $SD = 1.93$), $t(41) = -2.60$, $p = 0.013$, $d = 0.40$, $BF_{10} = 3.22$, and *cued self-generation* ($M = -1.91$, $SD = 2.26$), $t(41) = -6.10$, $p < 0.001$, $d = 1.01$, $BF_{10} = 50{,}782.42$ (see Appendix 1, Table A1.1 for detail). N1 amplitudes of the *cued self-generation* condition were also found to be less negative than those of both *cued listening*, $t(41) = 2.87$, $p = 0.006$, $d = 0.51$, $BF_{10} = 5.85$, and *uncued self-generation*, $t(41) = 3.57$, $p < 0.001$, $d = 0.62$, $BF_{10} = 32.19$. Amplitudes of the N1 in the *uncued self-generation* and *cued listening* conditions were not found to differ significantly, $t(41) = 0.47$, $p = 0.639$, $BF_{10} = 0.19$.

Fig. 2.2. Results from Experiment 1



A. Auditory evoked potentials for Experiment 1, including pooled mean amplitudes at Fz, FCz and Cz, as well as ribbons representing 95% CIs. **B.** Mean voltages and 95% CIs for N1 (left) and P2 (right) by condition. Significant contrasts are indicated with their corresponding *p*-value. N1 amplitudes reflect pooled recordings at Fz, FCz and Cz, while P2 amplitudes reflect those at FCz, Cz and CPz. **C.** Topographic voltage maps for N1 (left) and P2 (right) components, with corresponding condition labels and legend for panels A and B. **D.** Key within-subject contrasts of N1 amplitude with mean difference and 95% CIs. These include contrasts illustrating the sensory attenuation effect (i.e., self- vs. external) without controlling for temporal predictability or control (*uncued self-generation* vs *uncued listening*), the effect of temporal predictability (*cued listening* vs *uncued listening*), the effect of temporal control (*uncued self-generation vs* *cued self-generation*) and sensory attenuation controlling for both temporal predictability and control (*cued self-generation vs cued listening*).

2.3.2.2 P2

A one-way repeated measures ANOVA identified significant differences between the mean amplitudes (μV) of P2 components across conditions, $F(3, 123) = 9.486$, $p < 0.001$, partial $\eta^2 = 0.188$, $BF_{10} = 4902.41$. Pairwise comparisons suggested that the amplitudes of P2 in the *uncued self-generation* condition ($M = -0.14$, $SD = 2.88$) were significantly less than those of the *cued self-generation* ($M = 1.73$, $SD = 2.96$), $t(41) = -3.46$, $p = 0.001$, $d = 0.64$, $BF_{10} = 24.31$, *uncued listening* ($M = 2.18$, $SD = 3.10$), $t(41) = -4.44$, $p < 0.001$, $d = 0.78$, $BF_{10} = 352.03$, and *cued listening* ($M = 2.52$, $SD = 2.94$), $t(41) = -4.34$, $p < 0.001$, $d = 0.92$, $BF_{10} = 261.99$, conditions. The P2 amplitudes of the other conditions did not significantly differ from each other (see Appendix 1, Table A1.2 for detail).

2.3.2.3 Behavioural data

A paired samples Student's *t*-test was used to compare participants' accuracy in pressing the keyboard button to synchronise with visual stimuli in the two cued conditions. Results suggested that mean error (*ms*; i.e., averaged across all trials for each participant) in the *active cued* condition ($M = -73.36$, $SD = 41.15$, max = 104.39) and the *motor cued* condition ($M = -81.47$, $SD = 40.72$, max = 96.24) did not differ significantly from each other, $t(41) = 0.93$, $p = 0.358$, $BF_{10} = 0.25$.

2.3.2.4 Power analyses

Post hoc analyses explored the power of the sample in Experiment 1 ($n = 42$) to detect small ($d = 0.2$), medium ($d = 0.5$), and large ($d = 0.8$) effects, according to standardised reporting conventions (Cohen, 1992). Power ($1 - \beta$) varied based on the impact of correction for multiple comparisons, and included a range for small (0.05 to 0.24), medium (0.58 to 0.89) and large (0.98 to 1.00) effects.

2.3.3 Discussion

Through analysis of the contrasts, we were able to isolate the effects of temporal predictability and temporal control from one's input to generating sensations (see Table 2.1). As hypothesised, N1 amplitude in the *cued listening* condition was found to be significantly less negative than in *uncued listening*. This is consistent with previous research demonstrating that an increase in the temporal predictability of stimulus is associated with a reduction in neurophysiological response (e.g., Lange, 2009; Schafer & Marcus, 1973; Weiskrantz et al., 1971). In addition, the classic sensory attenuation effect was replicated in that smaller N1 amplitudes were observed in the *uncued self-generation* condition compared with *uncued listening*. Despite this, the N1 amplitude of the *uncued self-generation* condition was not found to differ significantly from that of *cued listening,* and the associated Bayes factor provided substantial evidence in favour of the null hypothesis (Jeffreys, 1998). This result suggests that the classic sensory attenuation effect may be eliminated by controlling for temporal predictability without also accounting for temporal control.

Critically, reduced N1 amplitudes were observed in the *cued self-generation* condition compared with *cued listening*. A reduced neurophysiological response to self-generated stimuli was therefore evident when the *self-generation* and *listening* conditions were matched in terms of both temporal predictability and temporal control. This result suggests that the phenomenon of sensory attenuation prevails when controlling for differences in both temporal predictability and temporal control, but may otherwise be conflated with the effect of temporal predictability alone. Of significance, N1 amplitudes elicited by tones in the *cued self-generation* condition were significantly smaller than in the *uncued self-generation* condition, owing to an apparent amplification related to temporal control. As reflected in the contrast between *uncued self-generation* and *cued listening*, the scale of this amplification was such that sensory attenuation (i.e., the difference in neurophysiological response between self- and externally generated stimuli) was diminished for stimuli over which participants exerted temporal control.

Although the functional significance of the P2 is relatively poorly understood, research has identified that it is influenced by factors that are both common to and differentiable from those affecting the N1. Heightened attention to stimuli has long been associated with a negativity that manifests as simultaneous enhancement of the N1 component and suppression of the P2; an effect described variously as ‘Processing Negativity’ (Näätänen et al., 1978) and ‘Nd’ (Hillyard et al., 1973). More negative N1 and P2 amplitudes in the *uncued self-generation* condition, relative to *cued self-generation*, may thereby reflect heightened auditory attention when participants had control over the timing of the stimuli. Although recent evidence suggests that P2 amplitude may be positively correlated with one’s sense of agency over sound (Timm et al., 2016), it is noteworthy that control over the timing of stimuli was associated with smaller P2 amplitudes in the present study. A potential reason for this discrepancy is that the study by Timm et al. (2016) used an illusion to examine the effects of perceived ownership (i.e., by making self-generated tones appear as if they were not a result of participants’ actions). In contrast, the present investigation explored effects involving temporal control (i.e., agency in determining when to generate a stimulus; see Haggard, 2017). Significantly, Timm et al. (2016) also observed reduced P2 amplitudes for self-generated tones compared with externally-generated tones when participants were not subject to the illusion of non-ownership.

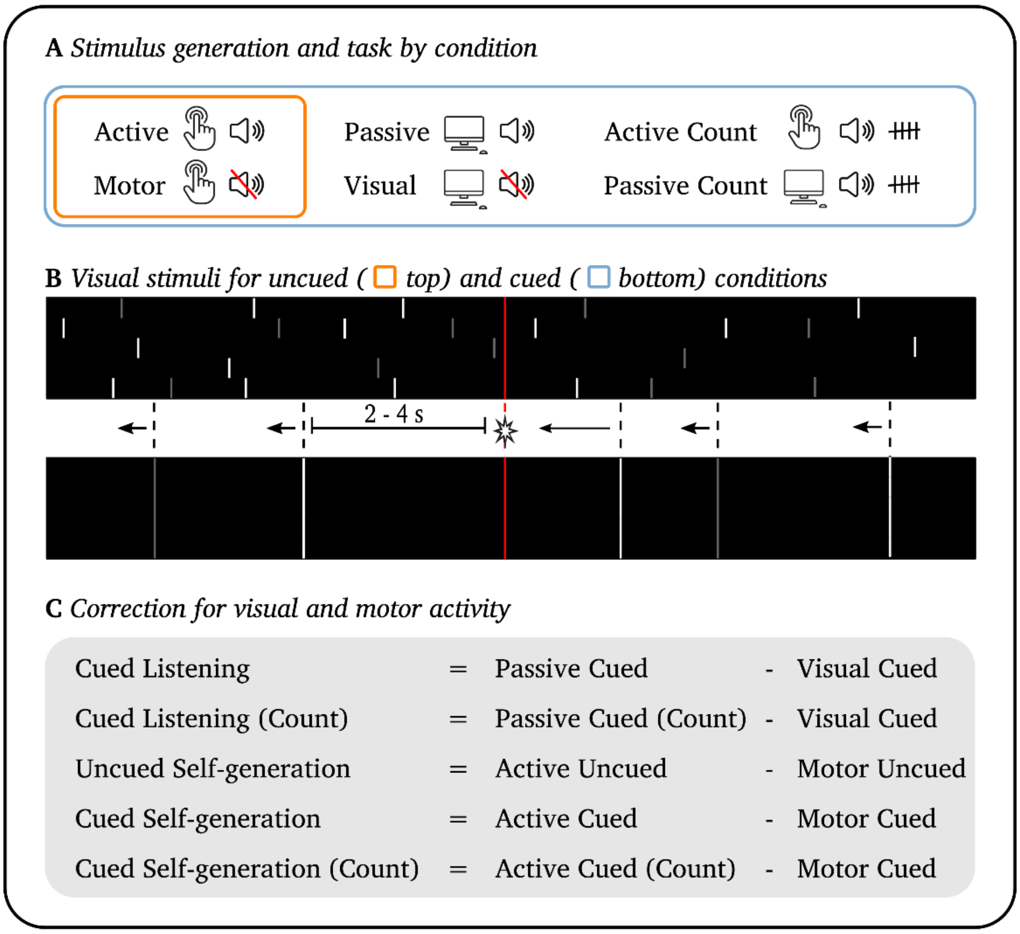
Potential discrepancies in the allocation of selective attention present a possible confound to the results of Experiment 1. Previous research has demonstrated amplification of the auditory N1 in tasks that required attention to auditory stimuli, compared to conditions in which attention was directed to visual stimuli (Hackley et al., 1990; Woods et al., 1992). If the *cued self-generation* condition involved heightened attention to visual stimuli in order to accurately time each button press, compared with *cued listening*, this may account for a reduced N1 amplitude in the former. To assess this possibility, the second experiment sought to both replicate key findings of Experiment 1 and quantify the effect of manipulating selective attention to the visual stimuli.

2.4 Experiment 2

In Experiment 2, we aimed to investigate the effect of selective attention on the auditory N1 amplitude. We focussed, in particular, on the effects of selective attention in differences between the *cued listening* and *cued self-generation* conditions. This contrast, which we describe as *sensory attenuation (controlled),* allows direct comparison of sensory responses to self- and externally-generated stimuli while holding constant the level of temporal predictability and temporal control. In Experiment 2, the potential effect of selective attention on the auditory evoked potential was explored by modifying task requirements such that similar levels were allocated to visual stimuli in variants of both the *passive cued* and *active cued* experimental conditions.

A proportion of the lines/line segments in the visual stimuli were changed from white to light grey (see Fig. 2.3B). With this exception, the *active uncued, active cued* and *passive cued* conditions were collected with identical procedures to Experiment 1. An additional two conditions were included that required participants to keep a tally of the number of long white or grey lines, and to report this at the conclusion of relevant blocks. These included the *active cued (count)* and *passive cued (count)* conditions. The contrast of the grey lines was such that they were difficult to distinguish until they approached the fixation line.

Fig. 2.3. Experiment 2 visual stimuli and schematic



A. Participants pressed a keyboard button to initiate events in the *active, active (count)* and *motor* conditions, while events were externally-generated (by computer) in the *passive, passive (count)* and *visual* conditions. Events involved an 85 dB tone (1000 Hz) in the *active, active (count), passive* and *passive (count)* conditions, while silent audio tracks marked events in the *motor* and *visual* conditions. Orange and blue boxes indicate the stimulus generation conditions (panel A) that were paired with *uncued* and *cued* conditions, respectively (panel B). *Uncued* and *cued* variants were presented for *active* and *motor* conditions, while other conditions involved only *cued* variants. **B.** The two *uncued* conditions were identical to corresponding conditions in Experiment 1, except that half of the line fragments were grey while the other half were white. These were the *active uncued* and *motor uncued* conditions. In six *cued* conditions, a proportion of lines were also made grey. This was done such that half of the lines were grey across the course of the experiment, while the exact proportion varied slightly within individual blocks. The *active cued, motor cued, passive cued* and *visual cued* conditions were otherwise identical to Experiment 1, with participants instructed to ignore variation in line shading. The *active cued (count)* and *cued passive (count)* conditions were similar to *active cued* and *passive cued*, respectively, except that participants were required to keep a mental tally of the number of target lines (i.e., white or grey) and report this at the conclusion of the block. **C.** The eight experimental conditions supported development of five analysis conditions: *cued listening, cued listening (count), uncued self-generation, cued self-generation*, and *cued self-generation (count)*.

An analysis of the anterior N2 component (N2b) was used as a manipulation check of increased attentional load in the counting task. This component is observed in frontocentral regions between 200 ms and 350 ms post-stimulus on tasks that involve cognitive control and manipulations of cognitive load (Folstein & Van Petten, 2008). The N2b can be distinguished from other components by its sensitivity to the level of attention allocated to stimuli (Pritchard et al., 1991) and insensitivity to stimulus probability (Luck & Hillyard, 1994). In addition, the N2b has been associated with response inhibition tasks, including the ‘go/no-go’ paradigm (Donders, 1969), in which participants are required to respond to one stimulus while withholding their response to others (Bruin & Wijers, 2002). Importantly, it has also been found to be influenced by similar tasks requiring only mental responses, such as counting target stimuli (Mertens & Polich, 1997). We therefore hypothesised that conditions requiring participants to keep tally of the number of target lines would elicit larger N2b components than conditions that did not involve counting.

2.4.1 Method

2.4.1.1 Participants

A further 38 healthy participants (25 females), aged between 17 and 36 years (*M* = 21.38, *Mdn* = 19.22, *SD* = 4.80), were recruited for Experiment 2. Participants were again recruited through the University of New South Wales (UNSW) electronic participants recruitment system (SONA), with approval provided for the study by the UNSW Human Research Ethics Advisory Panel (Psychology). Data from an additional four participants were collected but excluded from further analysis due to self-reported recreational drug use within the preceding 48 h (three participants) and self-reported diagnosis of a psychotic disorder (one participant).

2.4.1.2 Materials and design

EEG recording, data processing and statistical analyses were undertaken according to the same specifications as described for Experiment 1. Visual stimuli were adjusted, such that a proportion of white lines and line fragments were replaced by grey lines (see Fig. 2.3B). As with Experiment 1, a total of 90 trials were presented for each condition. Across three blocks, each containing 30 trials, a total of 14, 15 and 16 white lines (or equivalent line fragments) were presented. The *active uncued, active cued* and *passive cued* conditions, as well as their *motor* and *visual* controls, were collected according to the procedures described for Experiment 1. In these conditions, participants were instructed to disregard variation in line colour. Two additional conditions were included, which asked participants to count the total number of lines of a particular variety (i.e., white or grey) in addition to existing requirements. Shading of the white and grey lines was made such that they were difficult to distinguish until they approached the fixation line, and the order of white and grey lines was randomised within blocks.

Blocks were presented in three sets, each containing one block for each of the eight experimental conditions. The order of blocks was again pseudorandom, such that each set commenced with the *active uncued* condition. The line shade ratio of blocks was randomised across sets (i.e., different conditions were able to contain blocks with differing ratios for each set). The target line type (i.e., white or grey) was counterbalanced across participants. As such, eight separate conditions were administered, including two *uncued* (i.e., *active* and *motor*) and six cued (i.e., *active, passive, motor, visual, active count* and *passive count*). The waveforms for *active* and *passive* conditions (i.e., including the *count* conditions) were corrected for *motor* and *visual* effects, respectively, using the same method as described for Experiment 1. The resulting analysis conditions included *self-generation uncued, listening cued, listening cued (count), self-generation cued*, and *self-generation cued (count)*.

As in Experiment 1, at least 30 trials were obtained per participant for each of the eight conditions. A one-way repeated measures ANOVA was used to assess potential differences in the number of trials included in grand average waveforms between conditions. This included trial counts for *active uncued* (M = 88.53, SD = 4.05), *active cued* (M = 89.05, SD = 2.86), *active cued count* (M = 88.11, SD = 5.08), *motor uncued* (M = 87.03, SD = 6.92), *motor cued* (M = 89.34, SD = 2.22), *passive cued* (M = 89.00, SD = 2.25), *passive cued count* (M = 89.32, SD = 1.36) and *visual cued* (M = 88.55, SD = 2.72). Non-sphericity was identified by Mauchly’s test (Mauchly, 1940) and corrected using the Greenhouse-Geisser method (Geisser & Greenhouse, 1958). Results did not reveal a statistically significant difference in the number of trials between conditions, $F(3.23, 119.48) = 1.98$, $p = 0.117$, partial $\eta^2 = 0.051$, $BF_{10} = 0.31$.

The N1 component was identified as the most negative local minimum between 25 ms and 175 ms in the collapsed localizer waveform. This was found to occur 92 ms post-stimulus, with mean amplitudes calculated between 82 ms and 102 ms. The P2 component was again identified in the collapsed localizer waveform as the most positive local maximum between 110 ms and 200 ms, which was found to occur at 177 ms. P2 component amplitudes were therefore calculated based on recordings between 167 ms and 187 ms. Although P2 analyses are not reported in the main body, descriptive statistics and contrasts of each condition may be found in Appendix 1, Table A1.4. The N2b component was analysed using pooled recordings at the Fz, FCz and Cz electrode sites, reflecting its frontocentral topography. These sites were selected on the basis that, while varied, investigations of the anterior N2 have typically utilised frontal locations on the midline of the scalp (Näätänen & Picton, 1986). The N2b components were defined based on the collapsed localizer method, using pooled recordings from electrode sites Fz, FCz and Cz between 200 ms and 350 ms post-stimulus. The N2b component was found to occur at 317 ms, supporting calculation of component amplitudes between 307 ms and 327 ms.

2.4.2 Results

2.4.2.1 N1

The N1 peak was identified as having occurred 92 ms post-stimulus. Amplitudes of the N1 component (i.e., between 82 and 102 ms) were compared using a one-way repeated measures ANOVA. Results revealed a statistically significant difference between conditions, $F(3.11, 115.16) = 4.944$, $p = 0.002$, partial $\eta^2 = 0.118$, $BF_{10} = 30.23$. A series of paired samples Student’s t-tests identified that the mean amplitude (μV) of the *uncued self-generation* condition ($M = -3.05$, $SD = 1.61$) was significantly more negative than those of the *cued self-generation* condition ($M = -2.09$, $SD = 1.89$), $t(37) = -2.70$, $p = 0.010$, $d = 0.55$, $BF_{10} = 4.06$, and the *cued self-generation (count)* condition ($M = -2.14$, $SD = 1.57$), $t(37)$

= -3.00, p = 0.005, d = 0.57, BF_{10} = 7.87 (see Appendix 1, Table A1.3 for detail). Similarly, the *cued listening* condition (M = -3.18, SD = 1.88) was found to have larger (i.e., more negative) N1 components than those of the *cued self-generation* condition, $t(37)$ = -3.08, p = 0.004, d = 0.58, BF_{10} = 9.34, and *cued self-generation (count)* condition, $t(37)$ = -3.09, p = 0.004, d = 0.60, BF_{10} = 9.50. The *cued listening (count)* condition (M = -3.12, SD = 2.03) was also found to have larger N1 components than those of the *cued self-generation* condition, $t(37)$ = -2.85, p = 0.007, d = 0.52, BF_{10} = 5.55. However, the difference between N1 amplitudes in the *cued listening (count)* condition was not found to differ significantly from the *cued self-generation (count)* condition after correcting for multiple comparisons, $t(37)$ = -2.47, p = 0.018, p_{corr} = 0.055, d = 0.54, BF_{10} = 2.50. The N1 amplitudes of *cued self-generation* and *cued self-generation (count)* were not found to differ significantly, $t(37)$ = 0.18, p = 0.856, BF_{10} = 0.18, nor were those of *cued listening* and *cued listening (count),* $t(37)$ = -0.22, p = 0.828, BF_{10} = 0.18. Bayes factors representing the comparison of *cued self-generation* and *cued listening* conditions with their counting equivalents both represent substantial evidence in favour of null hypotheses (Jeffreys, 1998).

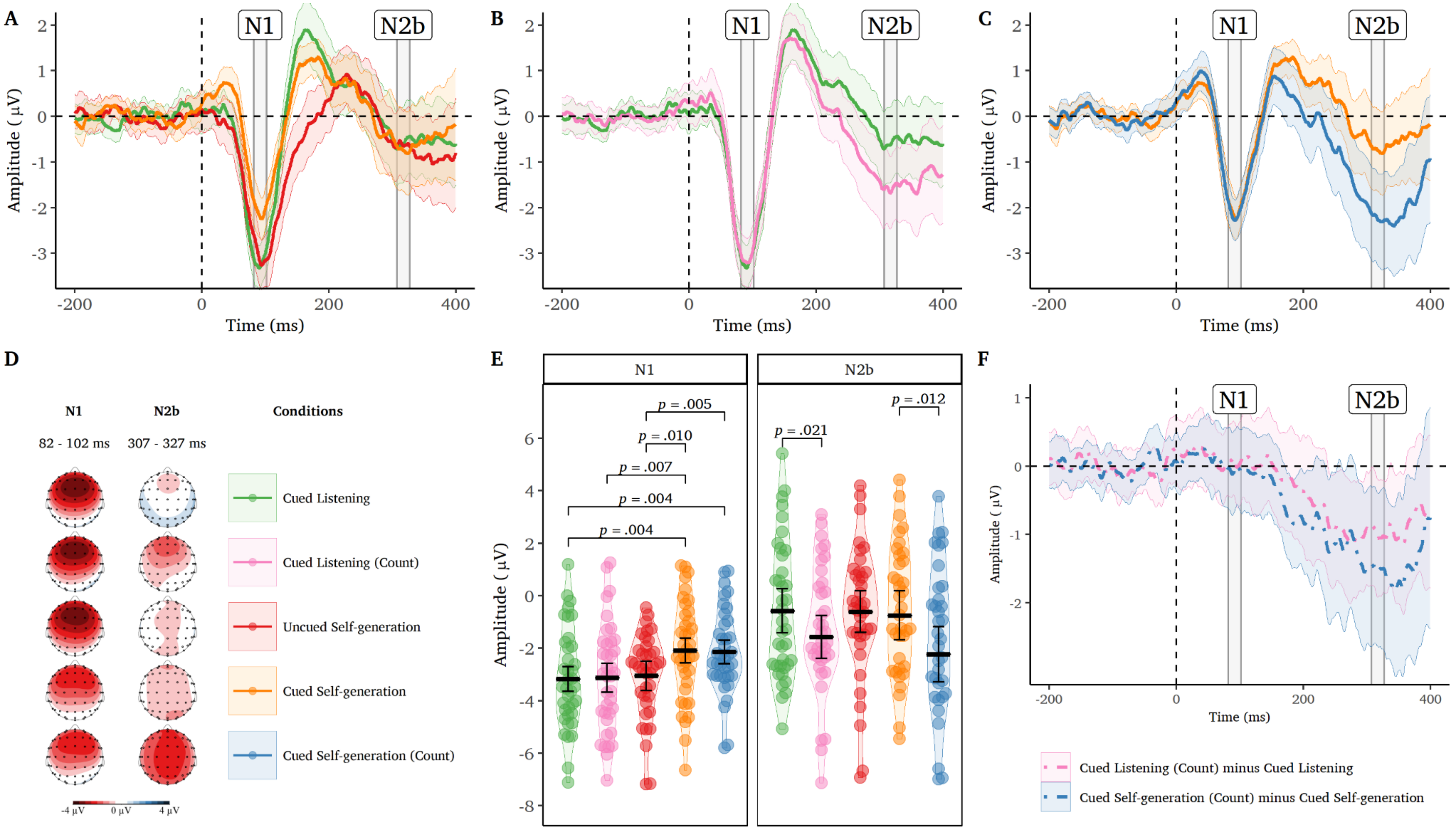
2.4.2.2 Anterior N2

The anterior N2 component (N2b) peak was found to have occurred 317 ms post-stimulus. Mean amplitudes were calculated in the same manner as for other components, based on a 20 ms window centred on this peak (i.e., between 307 ms and 327 ms). A one-way repeated measures ANOVA identified that the N2b component varied significantly across conditions, $F(2.85, 105.28)$ = 2.775, p = 0.043, partial η^2 = 0.07, BF_{10} = 1.41. Pairwise comparison revealed that the mean N2b amplitude (μV) of the *cued listening (count)* condition (M = -1.57, SD = 2.81) was significantly more negative than those of the *cued listening* condition (M = -0.57, SD = 2.58), $t(37)$ = -2.41, p = 0.021, d = 0.37, BF_{10} = 2.20 (see Appendix 1, Table A1.5 for detail). The N2b of the *cued self-generation (count)* condition (*M* = -2.23, *SD* = 3.32) was found to be significantly more negative than that of the *cued self-generation* condition (*M* = -0.75, *SD* = 2.70), *t*(37) = -2.65, *p* = 0.012, *d* = 0.49, BF_{10} = 3.62. The difference in N2b amplitude between *cued self-generation (count)* and the *uncued self-generation* condition (*M* = -0.61, *SD* = 2.48) was not found to be statistically significant following correction for multiple comparisons, *t*(37) = -2.46, *p* = 0.019, p_{corr} = 0.051, *d* = 0.56, BF_{10} = 2.44. Significant differences were not observed between the *cued listening (count)* condition and the *cued self-generation* condition, *t*(37) = -1.20, *p = 0.*238, BF_{10} = 0.34, the *cued self-generation (count)* condition, *t*(37) = -0.96, *p* = .826, BF_{10} = 0.27, or the *uncued self-generation* condition, *t*(37) = -1.79, *p* = 0.082, BF_{10} = 0.21. In addition, the difference between the *cued listening* condition and the *cued self-generation (count)* condition was not found to be significant following correction for multiple comparisons, *t*(37) = 2.13, *p* = 0.040, p_{corr} = 0.076, BF_{10} = 1.30.

2.4.2.3 Behavioural data

Participants' accuracy in keeping tally of the number of target lines in the *active cued (count)* and *passive cued (count)* conditions was calculated as the error rate (i.e., absolute difference between reported and actual number of target lines per block), averaged across the three blocks. Participants were found to demonstrate a high level of accuracy (i.e., low number of errors) in both the *active* (*M* = 0.47, *SD* = 0.55, max = 2.33) and *listening* (*M* = 0.42, *SD* = 0.67, max = 3.33) variants, and participants' accuracy did not differ significantly between these two conditions, *t*(37) = 0.42, *p* = 0.676, BF_{10} = 0.19. ISIs and the synchrony of participants' button press to passing lines were assessed in the same manner as Experiment 1 and not found to differ between *cued* conditions (see Appendix 1 for detail).

Fig. 2.4. Results from Experiment 2



A to C. Auditory evoked potentials for Experiment 2, including pooled mean amplitudes of Fz, FCz and Cz, as well as ribbons representing 95% CIs. Panels present (A) conditions replicating those of Experiment 1, including *cued listening, uncued self-generation* and *cued self-generation*, (B) *cued listening* and *cued listening (count)* (C) *cued self-generation* and *cued self-generation (count)*. **D.** Topographic voltage maps for the N1 and N2b latency window, with corresponding condition labels and legend for panels A to C and and E to F. Significant contrasts are indicated with their corresponding *p*-value. **E.** Mean voltages and 95% CIs for the N1 (left) and N2b (right) components, by condition. **F.** Difference waves comparing *cued listening (count)* and *cued self-generation (count)* with their non-counting equivalents (*cued listening* and *cued self-generation*, respectively).

2.4.2.4 Power analyses

Post hoc analyses explored the power of the sample in Experiment 2 (*n* = 38) to detect small (*d* = 0.2), medium (*d* = 0.5), and large (*d* = 0.8) effects, according to standardised reporting conventions (Cohen, 1992). Power (1 - β) varied based on the impact of correction for multiple comparisons, and included a range for small (0.02 to 0.22), medium (0.40 to 0.85) and large (0.93 to 1.00) effects.

2.4.3 Discussion

The effects of *temporal control* and *sensory attenuation (controlled)* were replicated from Experiment 1, with attenuation of N1 amplitudes in the *cued self-generation* condition relative to the *uncued self-generation* and *cued listening* respectively. Differences in N1 amplitude were not observed between the *cued self-generation* and *cued self-generation (count)* conditions, or between the *cued listening* and *cued listening (count)* conditions, and the associated Bayes factors provided substantial evidence in support of the null hypotheses. In contrast, anterior N2 component amplitudes in the *cued self-generation (count)* and *cued listening (count)* conditions were larger (i.e., more negative) than those in equivalent conditions that did not require counting. This was consistent with hypotheses, reflecting effective manipulation of attentional load such that demand for visual attention was greater when participants were required to keep tally of the target lines.

The fact that increased demand for visual attention was not associated with a reduction in N1 amplitude suggests that the observed differences between the *cued listening* and *cued self-generation* conditions are not likely to be driven by differences in selective attention. It is noteworthy that these findings are consistent with previous research that has demonstrated a sensory attenuation effect that is insensitive to manipulation of attention to visual stimuli (Timm et al., 2013). Insensitivity of N1 amplitudes to increased visual attention within the *cued self-generation (count)* condition may indicate that the difference between *cued self-generation* and *uncued self-generation* is also unlikely to be attributable to differences in attentional demand. Future research could explore this possibility by using a similar paradigm to draw attention towards visual stimuli during the *uncued self-generation* condition.

2.5 General discussion

The present study investigated effects associated with temporal predictability and temporal control on the neurophysiological response to self- and externally-generated auditory stimuli. While temporal predictability and temporal control were each shown to affect N1 amplitude, the contrasting nature of these effects meant that the phenomenon of sensory attenuation prevailed when controlling for both. That is, self-generated sounds elicited a smaller cortical response compared with externally-generated sounds when controlling for both temporal predictability and temporal control. Consistent with previous research (Lange, 2009; Schafer & Marcus, 1973; Sowman et al., 2012; Weiskrantz et al., 1971), increasing the temporal predictability of sound stimuli was found to reduce the amplitude of the auditory N1 component. This finding sits within a broader literature demonstrating that the sensory nervous system responds less to stimuli that are more highly predicted (Friston, 2005, 2010). In contrast to the suppressive effect of temporal predictability, a positive relationship was observed between participants' temporal control of self-generated sound and resulting N1 component amplitude. To our knowledge, this effect has not previously been reported. Interestingly, the magnitude of effect was such that the difference in N1 component amplitudes elicited by self- and externally-generated stimuli was diminished when participants had temporal control. We replicated this effect in Experiment 2, which also explored the potential influence of changes in selective attention. We found that changing task requirements to increase selective visual attention in both the *self-generation* and *listening* conditions did not result in a change to the observed pattern of N1 amplitudes.

By suppressing one's neurophysiological response to self-generated stimuli, compared to those created externally, sensory attenuation is believed to serve an adaptive role in removing from our perceptual experience information that can be anticipated on the basis of motor activity alone (Miall & Wolpert, 1996). An observed amplification of temporally-controlled sensations may therefore reflect increased utility of sensory information associated with stimuli that result from deliberately-controlled action, compared with those arising as incidental outcomes of movements. The sounds of one's own footsteps may be of less intrinsic value than someone else's while walking in an alley late at night. However, the sounds generated by one's own footsteps are likely to have more equal importance when attempting to walk quietly across creaky floorboards.

Increased activation of the sensory nervous system during volitional action is also consistent with the tenets of ideomotor theory, which proposes that action is generated through internal activation of its anticipated perceptual consequences (see review by Shin et al., 2010). Within this framework, it has been proposed that action is controlled differently based on whether it is guided by stimulus-response (sensorimotor) learning or through action-effect (ideomotor) learning (Herwig et al., 2007). Our results provide support to this notion, demonstrating increased activation of sensory cortices to stimuli resulting from intention-based action (i.e., *uncued self-generation*) compared to stimulus-based action (i.e., *cued self-generation*). A distinction between these forms of action may also be observed based on the neurological processes involved in their initiation. Recent research has demonstrated increased activation of the corticospinal motor system in response to external cues that have previously been associated with actions elicited by transcranial magnetic stimulation (Tran et al., 2019). Interestingly, this effect has been found to occur regardless of whether participants expect subsequent action (Tran et al., 2020).

With respect to the neuroanatomy supporting intention-based actions, these appear to be coordinated by structures within the posterior medial frontal cortex (pMFC; see review by Waszak et al., 2012). It is possible that effects associated with temporal control therefore reflect modulation of sensory cortical response by regions within the pMFC, including the supplementary motor area (SMA) and pre-supplementary motor area (pre-SMA). The SMA and pre-SMA have been implicated in a variety of timing functions (Wiener et al., 2010), including the internal production and discrimination of time intervals (Herrmann et al., 2014; Macar et al., 2006). Interestingly, the SMA has been associated with several functions of relevance to the phenomenon of sensory attenuation, including auditory processing (Rauschecker & Scott, 2009) and imagery (Mcnorgan, 2012), as well as a potential source of motor efference copies (Jürgens, 1984).

A potential alternative interpretation for the effect we have attributed to temporal control is that the effects of prediction based on external cues and self-generation are summative. Such an effect might mean that the difference between *uncued self-generation* and *cued self-generation* is attributable to the additional predictive information provided by external cues, as opposed to differences in temporal control. This may be consistent with recent evidence demonstrating that motor action serves to enhance temporal attention (Zalta et al., 2020) and the accuracy of temporal predictions (Morillon & Baillet, 2017). Future research is therefore needed to explore the manner in which the effects of internal predictions (e.g., based on internal forward models) combine with those of external cues.

Another potential avenue for future research may involve distinguishing effects resulting from volitional motor activation from higher-level appraisal of one's agency in the creation of stimuli. Weiss et al. (2011) proposed that the reduced subjective intensity of self-generated sounds when these were prompted by the experimenter resulted from the social interaction that this involved – an account that favours the role of one's perception of agency. In contrast, research by Reznik et al. (2014) identified an enhanced response in the auditory cortex when participants played simple melodies on a piano keyboard, compared with when these were passively observed. Because participants were required to generate these sounds according to set temporal sequences, it may be argued that enhancement in this context was more likely to have resulted from volitional motor activity than from a higher-level perception of agency. A possible extension to the present study that might help to delineate the effects of ideomotor control from those involving higher-level appraisal of agency may entail providing participants with temporal control over stimuli that are externally triggered. For example, this may be done by allowing participants to select a rhythm or temporal sequence for subsequent passive observation. Further research into the relationship between ideomotor control and perceptions of agency may also have relevance to understanding the pathological substrates of schizophrenia, which is characterised by distortions with respect to both agency (Frith et al., 2000b) and sensory attenuation (e.g., Pinheiro et al., 2013; Whitford, 2019).

2.6 Conclusion

Overall, our findings suggest that the phenomenon of sensory attenuation prevails when controlling for both temporal predictability and temporal control. At the same time, we demonstrate that these factors have differential effects on auditory-evoked activity. Increasing temporal predictability was found to reduce the auditory N1. This is consistent with past research, and suggests that the temporal predictability of self-generated stimuli may in many instances account for an observed reduction in neurophysiological response compared to externally-generated stimuli. Conversely, we observed and describe for the first time (to our knowledge) an apparent amplification of sensory response to stimuli that are under one’s temporal control. That is, the auditory N1 to stimuli elicited according to participants own timing was found to be larger than when they were required to generate these in response to visual cues. When compared with sensations that are generated by the actions of an external agent, self-generated sensations commonly differ with respect to both temporal predictability and temporal control. Results from the present investigation therefore necessitate a re-evaluation of the experimental paradigms used to study the phenomenon of sensory attenuation.

3. Exploring the internal forward model: Action-effect prediction and attention in sensorimotor processing

Submitted for publication:[1]

Harrison, A. W., Hughes, G., Rudman, G., Christensen, B. K., & Whitford, T. J. (under review). *Exploring the internal forward model: Action-effect prediction and attention in sensorimotor processing*.

3.1 Abstract

An observed reduction in the neurophysiological response to self- versus externally-generated stimuli (i.e., sensory attenuation) is often attributed to prediction-based internal forward models. Despite common focus on the auditory N1 in studies of sensory attenuation, there is limited evidence regarding its sensitivity to action-effect contingency (i.e., the probability of action eliciting a stimulus). Research is also needed to compare the use of prediction in sensorimotor processes relating to stimulus-driven and volitional movement. In this study (*N* = 64), we explored the influence of action-effect contingency on event-related potentials associated with visually-cued and uncued movement, as well as resultant stimuli. Our findings demonstrate that, despite an apparent role in motor preparation (i.e., indicated in readiness potential amplitude), action-effect contingency does not influence the primary cortical response to sound (i.e., N1 amplitude). Instead, we highlight evidence and explore electrophysiological markers suggesting that sensory attenuation involves suppressive attentional mechanisms.

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[1] This study has been posted as a preprint:
Harrison, A. W., Hughes, G., Rudman, G., Christensen, B. K., & Whitford, T. J. (2022). Exploring the internal forward model: Action-effect prediction and attention in sensorimotor processing. *PsyArXiv*. https://doi.org/10.31234/osf.io/rba67

3.2 Introduction

The term ‘sensory attenuation’ has been used to describe an observed reduction in the neurophysiological response and subjective intensity of sensations resulting from self-generated stimuli (e.g., Blakemore et al., 1998; Schafer & Marcus, 1973). This phenomenon is believed to reflect the activity of internal forward models (IFMs; Miall & Wolpert, 1996), in which duplicates of motor commands (i.e. 'efference copies'; von Holst & Mittelstaedt, 1950) are transmitted to sensory cortices and generate representations of the anticipated consequences of movement (i.e., 'corollary discharge'; Sperry, 1950). According to the IFM account, information arriving from sensory organs is compared with these predictions, allowing removal from one’s perceptual experience those sensations that may be predicted on the basis of motor activity alone (Miall & Wolpert, 1996). In this way, IFMs are believed to shape our perceptual experience to prioritise unanticipated stimuli and thereby remain vigilant to potentially important changes in our environment.

Beyond their influence on sensations resulting from self-generated stimuli, action-effect predictions are believed to play an integral role in the generation of movement. Ideomotor theory (James, 1890), which proposes that action is initiated through the internal activation of its anticipated sensory consequences, remains influential within the motor literature (see review by Shin et al., 2010). By integrating action and perception within a shared representational system (Hommel et al., 2001; Prinz, 1990; Prinz, 1997), the IFM is believed to facilitate both the prediction of future behavioural states and sensory consequences, as well as the selection of motor commands (Wolpert et al., 1995). Within this framework, one may select and initiate a motor action based on predictions regarding its sensory effects, then respond to observed discrepancies in resulting sensations to guide movement accordingly.

Despite an extensive corpus of research examining processes of sensorimotor integration, the role of action-effect prediction remains poorly understood. Reviews of the sensory attenuation literature have identified this limitation, for example, highlighting an absence of evidence to substantiate the central tenet that suppression of self-generated sensation depends on use of motor commands to predict stimuli (Horváth, 2015; Hughes et al., 2013b). Surprisingly few studies have directly investigated the influence of action-effect contingency on sensory response, particularly given the central role afforded to this form of prediction in the aforementioned theories of motor preparation and perception. Research into the effect of identity prediction (i.e., the ability to predict the precise nature of a stimulus; e.g., tone frequency in the case of sound) is particularly limited, and existing evidence is conflicted. While some data suggest that identity prediction may be associated with a reduced neurophysiological response to self-generated stimuli (Bäß et al., 2008; Darriba et al., 2021), other investigations have not always found this to be the case (Hughes et al., 2013a). For this reason, carefully-controlled research is needed to examine the effects of predictability on processes involved in sensorimotor integration.

With respect to the role of prediction in the generation of movement, an informative distinction has been made between motor actions involving stimulus-response and action-effect associations (e.g., Neumann, 1984). Evidence suggests that identical overt action may be guided by either form of learned association, depending on whether the action is stimulus-driven (i.e., responding to external stimuli) or volitional (i.e., selecting action based on its intended sensory effects; Herwig et al., 2007). It has been postulated that action-effect prediction may play a more central role in the production of volitional action (Herwig et al., 2007; Pfister et al., 2011), while stimulus-driven movement may be initiated as a form of prepared reflex in response to activating events (Hommel, 2000). Different mechanisms for the initiation of stimulus-driven and volitional action may be consistent with evidence that these forms of motor activity involve recruitment of differing neuroanatomical structures (see Fried et al., 2017). In addition, increased corticospinal excitability has been observed in response to cues that have previously been paired with action induced through transcranial magnetic stimulation (Tran et al., 2019). This has been found to occur irrespective of whether subsequent action is expected (Tran et al., 2020), providing further indications that action-effect contingency may be differentially recruited in the generation of stimulus-driven and volitional movement. Taken together, these findings highlight the need for research comparing the use of action-effect prediction in stimulus-driven and volitional movement.

In this investigation, we aimed to delineate the influence of action-effect contingency on motor preparation for stimulus-driven and volitional action, as well as the processing of resultant stimuli. To this end, we compared the pre- and post-stimulus event-related potentials (ERPs) of visually-cued (i.e., stimulus-driven) and uncued (i.e., volitional) movement, as well as effects associated with change in the likelihood of action eliciting auditory stimuli (see Fig. 3.1 for protocol schematic and visual stimuli). Pre-stimulus analyses focused on the readiness potential and lateralised readiness potential, as indices of motor preparation that have previously been investigated in research examining the role of action-effect contingency (Reznik et al., 2018; Vercillo et al., 2018; Wen et al., 2018). Post-stimulus analyses focused on the auditory N1, given the focus on this component in sensory attenuation research (e.g., Han et al., 2021; Han et al., 2022; Schafer & Marcus, 1973; Schröger et al., 2015). Interestingly, recent research has demonstrated reduced N1 amplitude to stimuli resulting from stimulus-driven action compared with those arising in response to volitional action (Harrison et al., 2021). Given theorised differences in the neural mechanisms of each form of action, and the role of identity prediction in the operation of IFMs, the sensitivity of this phenomenon to change in action-effect contingency was also considered a priority for investigation. We provide further detail regarding the functional properties of the RP, LRP and auditory N1 in the following section, as well as the specific hypotheses relating to each.

The readiness potential (RP) is a slow negative component that builds over motor areas in the lead-up to self-initiated movement (Kornhuber & Deecke, 1965) and is generally believed to represent the final stages of motor preparation (Shibasaki & Hallett, 2006). A diffuse variety of neural sources have been identified for the RP, including the primary motor, premotor and somatosensory cortices, the supplementary motor area (SMA) and pre-SMA, as well as the rostral and caudal cingulate motor areas (Jahanshahi & Hallett, 2003). Interestingly, RP amplitude has recently been found to be influenced by action-effect contingency, with larger potentials observed prior to actions associated with a higher probability of eliciting stimuli (Reznik et al., 2018; Vercillo et al., 2018; Wen et al., 2018). While findings provide evidence that action-effect prediction is involved in motor preparation, the precise mechanisms remain to be investigated, as well as potential differences with respect to the initiation of volitional and stimulus-driven movement. Given that preparation for volitional movement is believed to rely on the prediction of resulting sensations to a larger extent (Hommel, 2000), action-effect contingency was hypothesised to influence RP amplitude for this form of movement to a larger extent than for stimulus-driven action.

Unilateral hand movement is preceded by relative negativity over the contralateral hemisphere (Deecke et al., 1976). This activity, known as the lateralised readiness potential (LRP), can also be observed in moments following presentation of a cueing stimulus (Kutas & Donchin, 1980). The LRP is believed to derive largely from the primary motor cortex (de Jong et al., 1988) and is considered a subcomponent of the RP that indexes hand-specific response activation (Smulders et al., 2012). Through a subtraction method involving trials with movement of effector muscles on both the left and right side, the LRP may be dissociated from lateralised potential relating to other structural and functional asymmetries (Gratton et al., 1988). Evidence suggests that the LRP is influenced by the complexity of planned movement (Hackley & Miller, 1995), though not its forcefulness (Sommer et al., 1994). Unlike the centralised RP, the LRP has not been found to be influenced by action-effect contingency (Reznik et al., 2018; Vercillo et al., 2018). To our knowledge, the LRP has not previously been examined in research contrasting activity associated with volitional and stimulus-driven action. Research has, however, demonstrated recruitment of the SMA during volitional movement and not stimulus-driven action (Debaere et al., 2003). Given that the SMA is involved in preparation for more complex movement (see Goldberg, 1985), for which LRP amplitudes have also been found to be larger (Hackley & Miller, 1995), it was hypothesised that volitional movement would be associated with larger LRP amplitudes than stimulus-driven action.

The N1 is a large negative component that is commonly studied in sensory attenuation research (e.g., Klaffehn et al., 2019; Lange, 2011; Whitford et al., 2017). It is believed to comprise at least three subcomponents, originating in the supratemporal plane, superior temporal gyrus, and regions within the motor cortex and/or cingulate gyrus (Giard et al., 1994; Näätänen & Picton, 1987). One subcomponent, described as N1b (McCallum & Curry, 1980; Woods, 1995), is mostly reflected within the largest, frontocentral peak of the N1 wave and occurs approximately 70 to 150 ms following the onset of auditory stimuli (Sanmiguel et al., 2013). As a reliable indicator of both sound intensity (Mulert et al., 2005) and neurophysiological response within the primary auditory cortex (Zouridakis et al., 1998), the N1b (described henceforth simply as the N1) is commonly used in studies of acoustic perception. Significantly, the amplitude of the N1 produced by self-generated sounds has recently been found to be smaller when the eliciting action is stimulus-driven than volitional (Harrison et al., 2021). These differences were observed in a paradigm that involved predictable self-generated sound stimuli. To our knowledge, the impact of action-effect contingency on N1 amplitude has not been compared for volitional and stimulus-driven movement. Notably, Harrison et al. (2021) observed that N1 amplitudes elicited by sound stimuli produced through volitional action did not differ from those externally-generated stimuli when these were made predictable in time. This may suggest that the phenomenon of sensory attenuation is specific to reafferent signal associated with stimulus-driven action. In accordance with the IFM account, it was therefore hypothesised that action-effect contingency would have a larger suppressive effect on N1 amplitudes resulting from sound produced by stimulus-driven action compared with that of volitional movement.

3.3 Method

3.3.1 Participants

The final sample included 64 healthy participants (45 female, 18 male and 1 other), aged between 17 and 36 years (*M* = 20.09, *Mdn* = 19.16, *SD* = 3.01). Participants volunteered in exchange for course credit towards an undergraduate psychology unit at the University of New South Wales. Data from an additional three participants were collected but excluded from analyses dues to self-reported diagnosis of a psychotic disorder, uncorrected hearing impairment, and recreational substance use in the preceding 24 hours (i.e., one participant each).

3.3.2 Materials and Design

Participants were seated in front of a BenQ XL2420T monitor (24-inch, 1920 x 1080 resolution screen), at a distance of approximately 60 centimetres. They were fitted with Sennheiser HD201 headphones and an EEG cap containing 64 Ag/AgCl active electrodes connected to a BioSemi ActiveTwo system. These were positioned according to the extended 10:20 layout. A vertical electro-oculogram (EOG) was developed based on recordings at Fp1 and an electrode positioned below the left eye. A horizontal EOG was produced using recordings from electrodes placed adjacent to the outer canthus of each eye. Electrodes were also placed on the tip of participants' noses, as well as their left and right mastoids. Sampling was conducted at a rate of 2048 Hz, during which time CMS and DRL electrodes were used to provide grounding.

Participants were instructed to place their left and right index fingers on the 'd' and 'k' keys of a keyboard, respectively, and to maintain their gaze on a small white arrow at the centre of the screen. On each trial, the arrow would point either left or right to indicate which key participants were required to press. A vertical red (fixation) line, which had a width of 1 pixel, extended approximately 25mm above and below the arrow (i.e., for a total visual angle of approximately 5.4°).

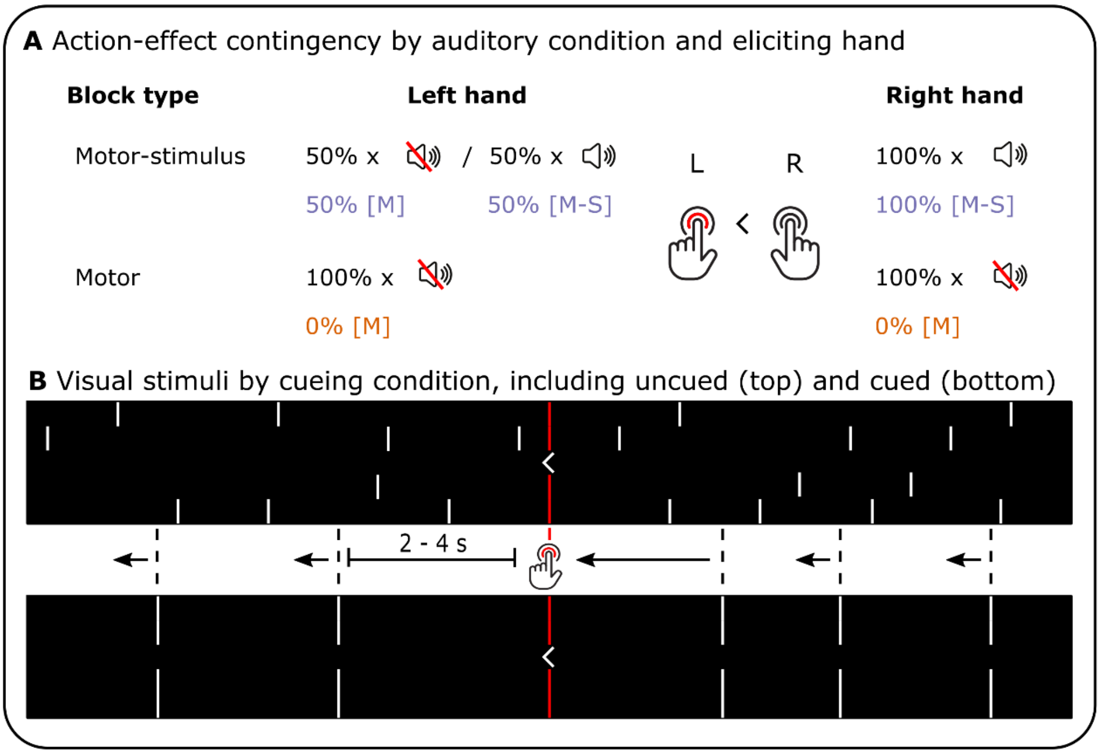
In two *uncued* block types (i.e., *motor-stimulus* and *motor*), a sequence of white line fragments appeared on the right side of the computer screen and moved leftward at a pace of approximately 3°/s (see Fig. 3.1B). The line fragments were of equal length and dispersed across four rows, spanning the height of the fixation line. While the outer two rows were adjacent, a gap that was equal in height to the arrow and each line fragment separated the inner two rows. They were one pixel wide and randomly distributed with a density that corresponded to approximately four fragments (i.e., one per row) every three seconds. Participants were asked to press the keyboard button indicated by the arrow at a time of their choosing, with a minimum of two seconds and a maximum of four seconds between each button press. They were asked to vary the interval between each press in an unpredictable manner. After each button press, the cueing arrow was removed following a delay of 600 ms and replaced with an arrow for the subsequent trial at 650 ms post-stimulus (i.e., removal and replacement was separated by a gap lasting 50 ms). In the event that participants pressed the wrong key for any given trial, a small red cross was displayed from 400 ms to 600 ms following the button press and the trial was excluded from analyses.

In *motor-stimulus* blocks, 100% of button presses with one hand elicited a tone via participant headphones. In contrast, tones were elicited by 50% of button presses with the other hand, while silent audio tracks were triggered to mark events on trials without sound. Two tone frequencies were used, including 85 dB SPL (A-weighted) pure tones (10 ms ramp, 100 ms duration) with frequencies of 1000 Hz (high pitch) and 500 Hz (low pitch). Tones and silent audio tracks were preloaded to an AudioFile Stimulus Processor (Cambridge Research Systems). Combinations of tone frequency (i.e., high and low), probability (i.e., 100% and 50%) and hand (i.e., left and right) were counterbalanced across participants. Each block involved 20 trials with 100% probability (i.e., for 20 tone presentations) and 40 trials with 50% probability (i.e., for 20 tone presentations and 20 silent audio tracks) in randomised order. The *uncued motor* block was identical to the *uncued motor-stimulus* block, including the order of left- and right-hand trials, except that all trials involved presentation of silent audio tracks. Each trial in these blocks contributed to the *uncued motor 0%* condition. Participants were informed regarding the probabilities of eliciting tones with their left and right hands prior to each block (i.e., for both *motor-stimulus* and *motor* block types).

In two *cued* block types (i.e., *motor-stimulus* and *motor*), participants again fixed their gaze on a small arrow located within a gap at the centre of the fixation line. A series of white (stimulus) lines, also with a gap at their centre, moved from right to left at a rate of approximately 3°/s (see Fig. 3.1B). These lines were spaced according to the timing of participants' button presses in the preceding *uncued motor-stimulus* block. The order of arrows indicating use of their left and right hand was similarly matched. Participants were instructed to press the corresponding button at the precise moment that each stimulus line intersected with the fixation line, meaning that the interval between button presses for *uncued* and *cued* conditions was made equal. As with the *uncued* conditions, button presses in the *cued motor-stimulus* block elicited a tone in 100% of trials for one hand and 50% of trials for the other. The probability and frequency of tones allocated to each participant's left- and right-hand button presses was the same for all *motor-stimulus* conditions in the experiment. The *cued motor* block was again identical, except that each button press triggered the presentation of a silent audio track.

The two *motor-stimulus* block types (i.e., *cued* and *uncued*) were repeated six times each, while the *motor* block types (i.e., *cued* and *uncued*) were repeated twice. As such, there was a total of 16 blocks supporting collection of 120 trials for each of the eight experimental condition types (i.e., *uncued* and *cued* variants of the *motor-stimulus 100%*, *motor-stimulus 50%*, *motor 50%*, and *motor 0%* conditions).

Fig. 3.1. Protocol schematic and visual stimuli



A. Participants pressed a keyboard button with the index finger on either their left or right hand, based on the direction indicated by an arrow at their point of fixation. In *motor-stimulus* blocks (i.e., trial types indicated in violet text on the top row), each press with one hand elicited a tone with 100% probability. Each press with the other hand had a 50% chance of eliciting a different tone and a 50% chance of triggering a silent audio track to mark the event. In *motor* blocks (i.e., trial types indicated in orange text on the bottom row), button presses with each hand elicited the silent audio track. Motor and motor-stimulus trial types are denoted ‘M’ and ‘M-S’ respectively, and will be referred to in this manner henceforth. **B.** In *uncued* blocks, participants were presented with a series of white line fragments across four rows. While the outer two rows were adjacent, a gap that was equal in height to the arrow and each line fragment separated the inner two rows. These fragments moved from right to left at a constant rate and were randomly distributed with a density that corresponded to four fragments (i.e., one per row) every three seconds. Participants fixed their gaze on an arrow at the centre of the screen, which was positioned within a small gap in a vertical red (fixation) line. They were instructed to press the required button every two to four seconds, at will and with unpredictable timing. In *cued* conditions, participants were presented with a series of white (stimulus) lines that moved from right to left at a constant rate. The spacing of these lines was based on the interval between participants’ button presses in the preceding *uncued motor-stimulus* block. Participants were instructed to press using the hand indicated at the precise moment that each stimulus line intersected with the fixation line. Uncued and cued blocks were matched in terms of the order of button presses, as well as whether each trial elicited a tone or silent audio track.

3.3.3 EEG Processing and Analysis

Data were referenced offline to the average of the mastoid electrodes and processed using BrainVision Analyzer. A phase-shift free half-amplitude Butterworth band-pass filter (0.1 Hz to 30 Hz) with 12 dB/Oct slope was applied, as well as a notch filter (50 Hz). Data were segmented into epochs beginning 1500 ms prior to each event and ending 1500 ms post-onset (i.e., 3000 ms segments). Eye movement artefacts were corrected using the method described by Miller et al. (1988), based on the approach developed by Gratton et al. (1983). With regard to artifact rejection, channel epochs were excluded if they were found to contain peak-to-peak amplitudes in excess of 200 µV between -1500 ms and 500 ms. Trials in which participants pressed the wrong key or pressed with an inter-trial interval (ITI) of less than 1800 ms were removed from analyses. Cued condition trials were also removed if participants failed to press the required key within 200 ms of the moment in which the stimulus and fixation lines intersected. Descriptive statistics relating to ITIs are provided in Table A2.7.

Because each motor-stimulus block necessarily contained twice the number of trials involving 50% contingency, compared with 100% contingency, each 50% trial was twice as likely to be preceded by a button press with the same hand. As a result, lateralized activity in the baseline correction period risked systematically biasing results in analyses that considered all trials. To mitigate this outcome, lateralized analyses were based on a subset of trials in which each condition type had an equal probability of being preceded by a button press with the same hand. This was achieved by only including trials that were preceded by a motor-stimulus trial (i.e., one in which a tone had been presented), of which there was an equal number of trials involving 50% and 100% contingencies.

Consistent with previous research (e.g., Pinheiro et al., 2020; Wohlert, 1993), baseline correction was applied for pre-stimulus analyses (i.e., RP and LRP) using the average voltage between -1500 ms and -1000 ms. Exploration of the data revealed lateralized activity in parieto-occipital regions commencing shortly before enactment (see Fig. 3.2D), which was subsequently investigated using a baseline correction period between -500 ms and -250 ms. Investigation of these particular effects, and therefore the selection of this window, were without precedent. However, the length of the correction window and stable voltage meant that observed effects were unlikely to be sensitive to the specific timeframe used. For N1 analyses, baseline correction was applied using the average voltage in the 200 ms prior to stimulus onset, in a manner consistent with similar studies (e.g., Harrison et al., 2021).

Summary statistics of the number of presented trials, behavioural exclusions and completed trials are presented by condition, including for both non-lateralized and lateralized analyses, in Table A2.8. It is noteworthy that, for both non-lateralized and lateralized analyses, marginally fewer trials were completed for cued conditions (M = 114.72, SD = 6.80) than for uncued conditions (M = 117.21, SD = 7.79). This was due to the exclusion of cued trials in which participants had failed to press the key to synchronise with passing stimulus lines.

Averaged waveforms were calculated based on a minimum of 41 useable trials, including for each of the eight experimental conditions in non-lateralized analyses (M = 115.75, Mdn = 118.00, SD = 7.45, min = 41) and subset of six experimental conditions in lateralized analyses (M = 75.93, Mdn = 76.00, SD = 6.75, min = 41). A 2 x 4 repeated measures ANOVA was conducted to compare the number of averaged trials included in *cued* versus *uncued* conditions and across *contingency* conditions (i.e., *100% [M-S]*, *50% [M-S]*, *50% [M]* and *0% [M]*) in the full set. The results revealed a statistically significant difference in the number of trials by *cueing* condition, $F(1, 63) = 24.41$, $p < .001$, $\eta_p^2 = .279$, BF_{10} = 6.37E+7. In particular, the average number of trials contained in *cued* condition waveforms (M = 114.51, SD = 6.86) was significantly small than in the *uncued* conditions (M = 117.00, *SD* = 7.80). Despite this, artefact rejection rates were similar for cued trials (M = 0.21%, SD = 0.85%) and uncued trials (M = 0.21%, SD = 0.74%), suggesting that this difference was due to the behavioural exclusions discussed above. Mauchly's test (Mauchly, 1940) indicated that the assumption of sphericity was violated with respect to the *contingency* conditions, necessitating correction using the Greenhouse-Geisser method (Geisser & Greenhouse, 1958). Following correction, the average number of trials was not found to differ significantly by *contingency* condition, $F(2.34, 147.43) = 0.28$, $p = .793$, $\eta_p^2 = .000$, $BF_{10} = 8.00E\text{-}03$. Similarly, the interaction between *cueing* and *contingency* was not found to be statistically significant, $F(1.25, 78.45) = 1.152$, $p = .299$, $\eta_p^2 = .018$, $BF_{10} = 2.00E\text{-}03$.

3.3.3.1 Readiness Potential

RP analyses were based on amplitude recordings at Cz, reflecting the central topography of the readiness potential. Two windows were examined, including from -1000 ms to -500 ms (early RP) and from -500 ms to 0 ms (late RP). These two windows have been differentiated in previous research as they are believed to involve discrete neural sources (e.g., Pinheiro et al., 2020; Vercillo et al., 2018; Wen et al., 2018). In particular, the early RP component is believed to involve bilateral activation of the SMA, while the late RP is believed to reflect the activity of the primary motor cortex that is predominant over the hemisphere that is contralateral to effector muscles (Oken & Phillips, 2009).

3.3.3.2 Lateralized Readiness Potentials

LRPs were examined using the method described by Coles (1989), which involves subtraction of amplitudes observed over the motor cortex on the side ipsilateral to effector muscles from those on the contralateral side (i.e., represented by electrodes C3 and C4). It is important to note that, because the allocation of probability conditions to each hand lasted the duration of the experiment, resulting LRPs represented only one direction of lateralisation for each participant. However, the direction of lateralisation was counterbalanced across participants, such that an equal number (*n* = 32) were lateralized in each direction (i.e., C3 and C4 were as frequently contralateral to effector muscles as they were ipsilateral for each condition). As with the N1 component, a 20 ms analysis window for the LRP was centred on the peak amplitude identified in a collapsed localiser waveform containing all conditions (Luck & Gaspelin, 2017). This was taken as the most negative local minimum between -200 and 0, which was found to have occurred at -70 ms.

3.3.3.3 Lateralized Enactment and Post-enactment Potentials

Two distinct maxima were also observed within the LRP collapsed localiser waveform (see Fig. 3.2D). The peaks of these lateralized effects were found to have occurred 1 ms and 107 ms post-stimulus, when taken as the most positive local maxima from -50 ms to 50 ms and 50 ms to 200 ms respectively. Examination of the topography of these effects, which we describe as the lateralized enactment potential (LEP) and lateralized post-enactment potential (LPP), suggested that they were substantially influenced by activity in parieto-occipital regions (see Fig. 3.2F). We utilised the same subtraction method as described for LRP analyses to isolate lateralized activity, with amplitude recordings at ipsilateral electrodes subtracted from those at equivalent contralateral locations. Counterbalancing across participants ensured that lateralized effects involving visual stimuli, for example, were distributed equally to contralateral and ipsilateral electrodes for all conditions. The LEP was found to be maximal when taken as the contrast between P5 and P6 electrodes, while the LPP demonstrated maximum amplitude at PO7 and PO8. Subsequent analyses therefore focussed on these electrodes.

3.3.3.4 Auditory N1

N1 component amplitudes were analysed using pooled recordings at electrode sites Fz, FCz and Cz, as has been done previously in recognition of the maximal N1 signal at these locations (Harrison et al., 2021; Näätänen & Picton, 1987; Whitford et al., 2017; Woods, 1995). To support comparison of these conditions in a manner that controlled for motor activity, *uncued [M-S]* and *cued [M-S]* conditions (i.e., both 50% and 100%) were corrected by subtracting the equivalent *0% [M]* conditions. Analyses were based on average recordings within a 20 ms window centred on the N1 component latency identified within a collapsed localiser waveform (i.e., averaging across all participants and conditions; Luck & Gaspelin, 2017). In particular, this was identified as the most negative local minimum between 25 ms and 175 ms post-stimulus in a collapsed waveform containing motor-corrected conditions – consistent with other similar studies of the auditory N1 component (Elijah et al., 2016, 2018; Harrison et al., 2021).The N1 peak was found to have occurred 94 ms after stimulus onset using this method, meaning that analyses involved average voltage recordings between 84 ms and 104 ms.

3.3.4 Statistical Analyses

3.3.4.1 Readiness and Lateralized Potentials

To mitigate the potential influence of differences within baseline correction periods, readiness potentials (i.e., RP and LRP) and lateralized effects (i.e., LEP and LPP) were analysed based on intermixed trial types contained in motor-stimulus blocks. This included *cued* and *uncued* variants of *motor-stimulus* trials (i.e., 100% and 50%) and *motor* trials (i.e., 50%). Component amplitudes were compared using a series of repeated measures analyses of variance (ANOVAs). These included main effects for *cueing* (i.e., cued vs uncued), as well as *contingency* (i.e., representing different motor and motor-stimulus variants). The contingency factor contained two orthogonal contrasts, supporting comparison of the 100% and 50% probability conditions, as well as the motor and motor-stimulus variants of the 50% conditions (see Table 3.1). These contrasts are henceforth described as the effects of *probability* and *action-effect*. As these were a priori contrasts and orthogonal, their statistical significance was not corrected for multiple comparisons. Bayes Factors were also produced for the effects contained within the ANOVAs, based on Cauchy priors with an r-scale of 1/√2 (Morey & Rouder, 2018). These Bayesian parameters have been recommended for use across a range of statistical procedures, including both regression (Gelman et al., 2008) and point null hypothesis testing (Jeffreys, 1998).

Table 3.1

Orthogonal contingency contrasts

	Contrast	
Condition	Probability	Action-effect
100% [M-S]	2	0
50% [M-S]	-1	1
50% [M]	-1	-1

Note. M-S denotes motor-stimulus conditions, while M denotes motor-only conditions.

3.3.4.2 Motor-corrected Auditory N1

A 2 x 2 repeated measures ANOVA was used to compare motor-corrected N1 component amplitudes (see *EEG Processing and Analysis*). In particular, this examined the main effects of *probability* (i.e., 50% vs. 100%) and *cueing* (i.e., cued vs. uncued), as well as their interaction. As with readiness and lateralized analyses, Bayes Factors were developed for the effects contained in this ANOVA based on Cauchy priors with an r-scale of 1/√2.

3.4 Results

3.4.1 Readiness and Lateralized Potentials

To analyse effects within readiness and lateralized potentials (i.e., early RP, late RP, LRP, LEP and LPP), 2 x 3 repeated measures ANOVAs were conducted to assess the main effect of *cueing* (i.e., cued vs uncued) and *contingency* conditions (i.e., 100% [M-S], 50% [M-S] and 50% [M]). Planned comparisons involved two orthogonal contrasts of *contingency* conditions, which supported the investigation of *probability* ([2, -1, -1]) and *action-effect* ([0, 1, -1]). Descriptive statistics relating to readiness potential amplitudes and those of the LRP are presented in Appendix 2 (Tables A2.1 and A2.2, respectively). Results of the ANOVAs and contrasts are also reported in full in Appendix 2 (Tables A2.4 and A2.5, respectively).

3.4.1.1 Readiness Potential

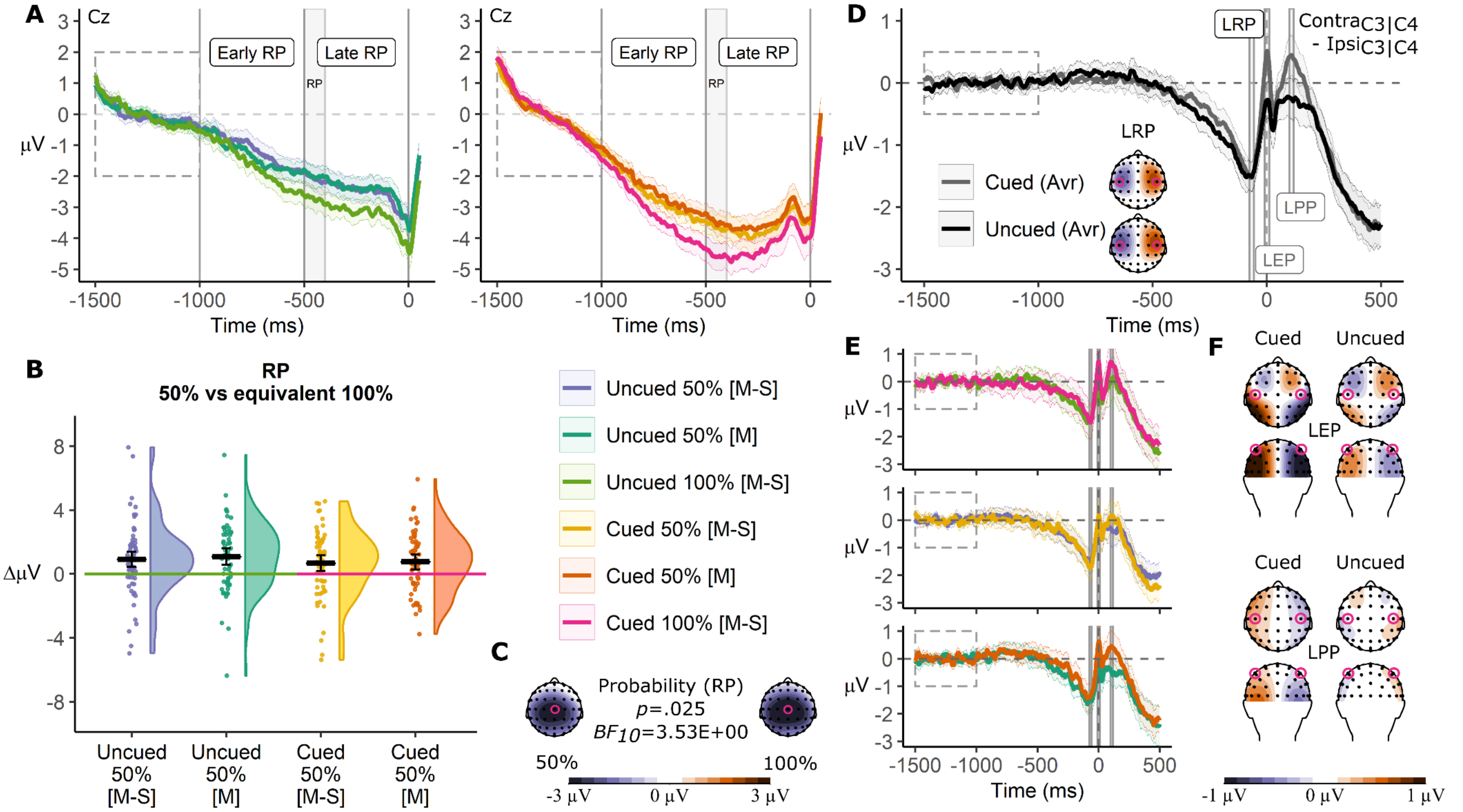
The ANOVAs revealed a significant main effect of *cueing* in both the early RP, $F(0.89, 56.06) = 31.34$, $p < .001$, $\eta_p^2 = 0.332$, $BF_{10} = 2.12\text{E}{+}15$, and late RP, $F(0.94, 59.38) = 7.47$, $p = .008$, $\eta_p^2 = 0.106$, $BF_{10} = 5.01\text{E}{+}03$ (see Fig. 3.2). For both early and late RPs, amplitude in the cued conditions were significantly more negative than for the uncued conditions. While the effect of *probability* was not found to be significant with respect to early RP amplitudes, $t(126) = 1.84$, $p = .069$, $d = 0.327$, $BF_{10} = 1.75\text{E}{+}00$, the mean amplitude of late RPs was found to be significantly larger (i.e., more negative) for the higher probability condition (i.e., 100%) compared to the lower probability (i.e., 50%) conditions, $t(126) = 2.17$, $p = .032$, $d = 0.386$, $BF_{10} = 7.82\text{E}{-}01$. Interactions between *cueing* and *probability* were not found to be statistically significant in relation to either the early RP, $t(189) = 0.77$, $p = 0.440$, $d = 0.113$, $BF_{10} = 0.13$, or late RP, $t(189) = -0.03$, $p = 0.973$, $d = -0.005$, $BF_{10} = 0.113$.

Late negative deflections were observed in RPs for both *uncued* and *cued* conditions (see Fig. 3.2A). These resembled the 'motor potential' subcomponent of the RP (Deecke et al., 1969), which commences approximately 80 ms prior to movement onset (Brunia et al., 2012). In *cued* conditions, this was preceded by a slow positive shift that may reflect 'pre-motor positivity' (PMP) or visual activity associated with approaching stimulus lines. Uncertainty regarding the precise nature of these effects motivated an additional analysis of RP amplitude using a window prior to their apparent commencement. A 2 x 3 repeated measures ANOVA on mean voltage recordings between -500 ms and -400 ms revealed a significant main effect of *cueing*, $F(0.92, 57.89) = 20.05$, $p < .001$, $\eta_p^2 = 0.241$, $BF_{10} =$ 1.67E+10. As with the late RP generally, the effect of *probability* was also significant in the narrowed window, $t(126) = 2.27$, $p = .025$, $d = 0.405$, $BF_{10} =$ 3.53E+00, with larger amplitude observed in the higher probability condition (i.e., 100%) compared with the lower probability conditions (i.e., 50%).

3.4.1.2 Lateralized Readiness Potential

With respect to LRP amplitude, the ANOVA did not reveal significant effects associated with *cueing*, $F(0.82, 51.79) = 0.01$, $p = .928$, $\eta_p^2 = <.001$, $BF_{10} =$ 1.16E-01, *contingency*, $F(1.31, 82.58) = 0.19$, $p = .829$, $\eta_p^2 = 0.003$, $BF_{10} =$ 3.72E-02, or their interaction, $F(1.64, 103.59) = 0.39$, $p = .677$, $\eta_p^2 = 0.006$, $BF_{10} =$ 6.62E-02. Planned contrasts were non-significant with respect to both *probability*, $t(126) = -0.22$, $p = .828$, $d = -0.039$, $BF_{10} =$ 1.19E-01, and *action-effect*, $t(126) = -0.07$, $p = .944$, $d = 0.010$, $BF_{10} =$ 1.31E-01.

Fig. 3.2. Readiness Potential and Lateralised Readiness Potential analyses



A. Grand-averaged recordings at Cz, demonstrating mean amplitude and 95% CI by uncued condition (left) and cued condition (right). **B.** Within-subject differences in late RP amplitude between 50% and equivalent 100% conditions (i.e., cued or uncued), with mean differences and 95% CIs. **C.** Topographic voltage maps demonstrating mean amplitude recordings by 50% and 100% conditions, with *p*-value and Bayes Factor representing the contrast effect of probability. **D.** Difference in grand-averaged recordings at C3 and C4 (i.e., contralateral minus ipsilateral), 95% CIs and LRP topographic voltage maps by cued and uncued condition (i.e., collapsing across probabilities). Note that, for consistency, electrodes were inverted along the sagittal plane for selected conditions by counterbalancing group. This was done such that topographic maps demonstrate lateralized effects as if each trial had involved a button press with the right hand. To remove activity not lateralized relative to the effector hand, unadjusted grand-averages (i.e., from all participants) were subtracted from unadjusted averages for each counterbalancing group prior to collation in the manner described. This had the effect of removing non-lateralized components, as well as unrelated lateralized activity (e.g., activity associated with visual attention) from topographic maps. **E.** Difference in grand-averaged voltage recordings at C3 and C4 (i.e., contralateral minus ipsilateral) for cued and uncued variants by probability condition, including 100% [M-S] (top), 50% [M-S] (middle) and 50% [M] (bottom). **F.** Topographic voltage maps by cued and uncued condition, representing mean voltage recordings at latencies corresponding to LEP (top) and LPP (bottom). Note that the same adjustments were applied based on counterbalancing group as described for panel D.

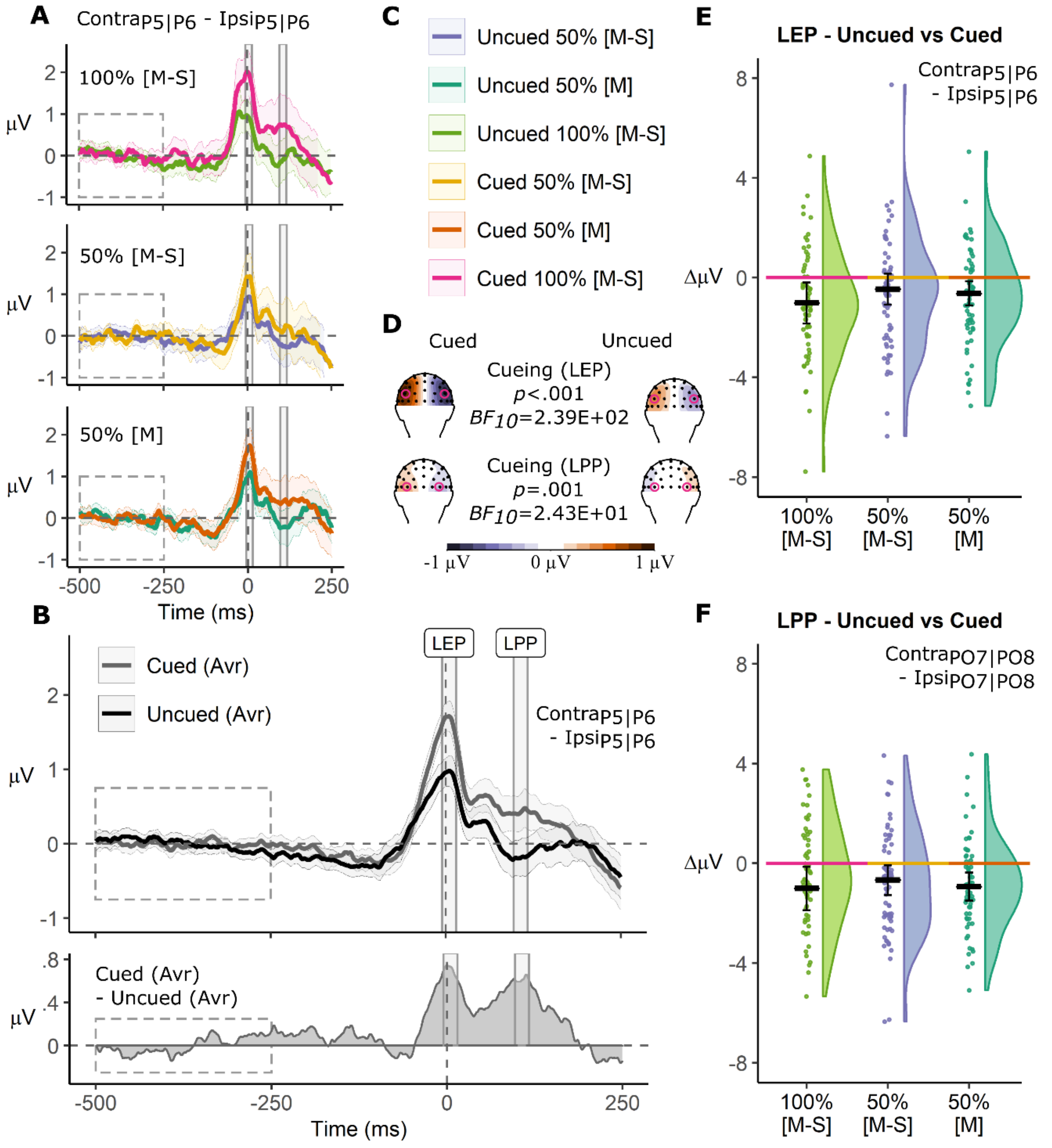
3.4.1.3 Lateralized Enactment and Post-enactment Potential

In the LRP waveforms, two distinct local maxima were observed at 1 ms and 107 ms post-action. Examination of topographic maps suggested that these were driven by lateralized potential with parieto-occipital positivity on the side contralateral to each trial's effector hand (see Fig. 3.2F). Subsequent analyses focussed on the locations at which these lateralized effects were maximal, averaging across participants and conditions. The peak of the first maximum, described henceforth as the lateralized enactment potential (LEP), was found to have occurred 4 ms post-action at P5/P6 (see Fig. 3.3B). Lateralized activity corresponding to the second observed peak (i.e., at C3/C4), described henceforth as the lateralized post-enactment potential (LPP), was found to be maximal at PO7/PO8. Because a distinct peak was not identified in the potential at these locations, analyses of this effect were based on the timing of the local maximum identified at C3/C4 (i.e., 107 ms post-action).

Another 2 x 3 repeated measures ANOVA was conducted to assess the main effects of *cueing* (i.e., cued vs uncued) and *contingency* (i.e., 100% [M-S], 50% [M-S] and 50% [M]) on the LEP. Orthogonal contrasts were again used to investigate the effects of *probability* and *action-effect*. Descriptive statistics relating to the lateralised potentials are presented in Table A2.2, while results of the ANOVAs and contrasts are reported in Tables A2.4 and A2.5 respectively (see Appendix 2). Results indicated a significant effect of *cueing* on LEP amplitude, $F(0.73, 46.29) = 24.60$, $p < .001$, $\eta_p^2 = 0.281$, $BF_{10} = 3.96E+02$, such that the LEP was larger (i.e., more positive) for *cued* conditions. In contrast, effects were non-significant with respect to *contingency*, $F(1.43, 89.80) = 0.80$, $p = .450$, $\eta_p^2 = 0.013$, $BF_{10} = 6.09E-02$, and the *cueing* x *contingency* interaction, $F(1.47, 92.59) = 0.74$, $p = .479$, $\eta_p^2 = 0.012$, $BF_{10} =$ 1.14E-01. Planned contrasts were also found to be non-significant, including both *probability*, $t(126) = 0.26$, $p = 0.799$, $d = 0.045$, $BF_{10} = 0.163$, and *action-effect*, $t(126) = -0.36$, $p = 0.722$, $d = -0.052$, $BF_{10} = 0.165$.

Results from analyses of the LPP mirrored those of the LEP. While a significant main effect was observed for *cueing*, $F(0.72, 45.27) = 10.49$, $p = .002$, $\eta_p^2 = 0.143$, $BF_{10} =$ 4.64E+01, non-significant results were observed with respect to the effect of *contingency*, $F(1.31, 82.62) = 2.36$, $p = .099$, $\eta_p^2 = 0.036$, $BF_{10} =$ 2.87E-01, and the *cueing* x *contingency* interaction, $F(1.44, 90.54) = 0.64$, $p = .528$, $\eta_p^2 = 0.01$, $BF_{10} =$ 8.74E-02. Planned contrasts were not found to be significant, including both *probability*, $t(126) = -0.95$, $p = .343$, $d = -0.17$, $BF_{10} = 0.858$, and *action-effect*, $t(126) = 0.1$, $p = .923$, $d = 0.014$, $BF_{10} =$ 1.28E-01.

Fig. 3.3. Lateralised enactment and post-enactment potential analyses

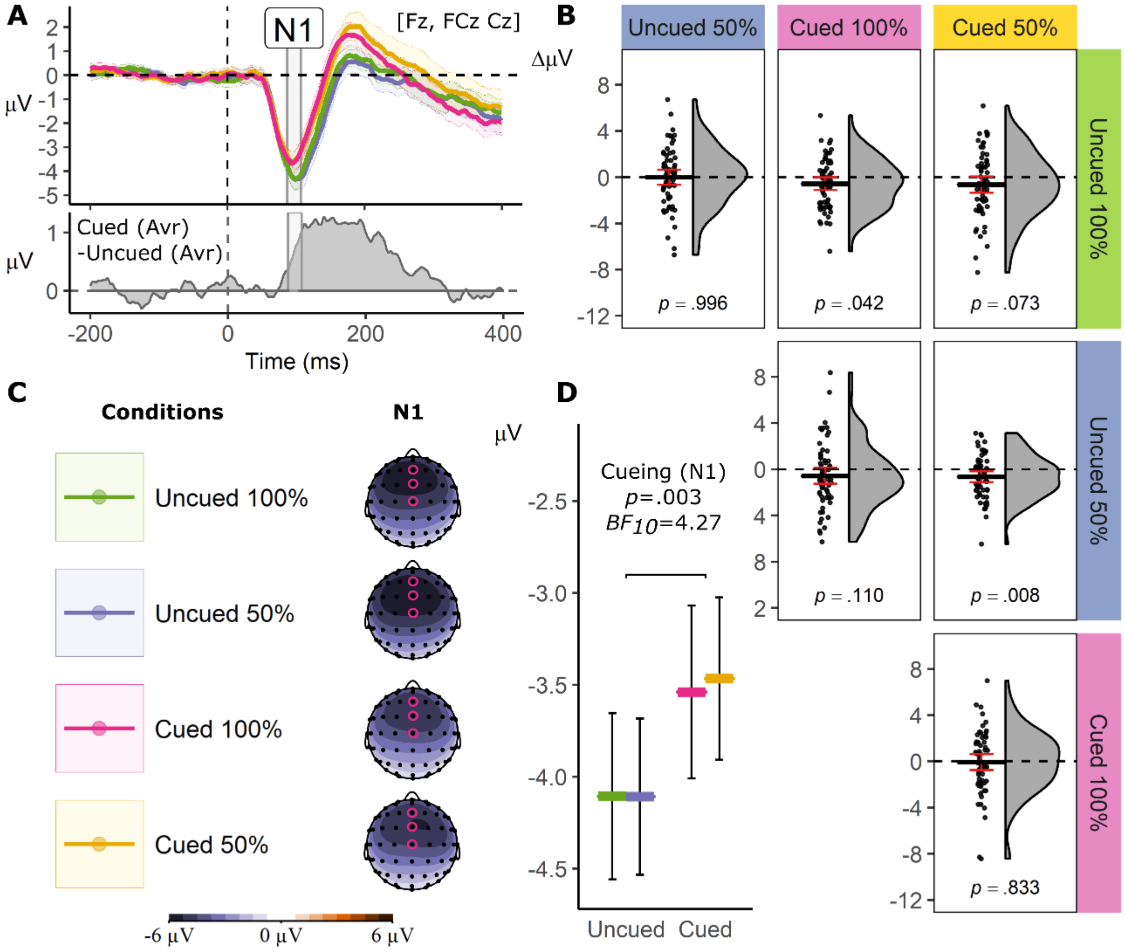


A. Difference in grand-averaged voltage recordings at P5 and P6 (i.e., contralateral minus ipsilateral) for cued and uncued variants by probability condition, including 100% [M-S] (top), 50% [M-S] (middle) and 50% [M] (bottom). **B.** Difference in grand-averaged voltage recordings at P5 and P6 (i.e., contralateral minus ipsilateral) and 95% CIs by cued and uncued condition (i.e., collapsing across probabilities; top). Difference between collapsed *cued* and *uncued* conditions (bottom). **C.** Legend for panels A, E and F. **D.** Topographic voltage maps representing mean amplitude recordings by cued and uncued condition, with *p*-values and Bayes Factors representing the main effect of cueing at latencies and electrodes corresponding to LEP (top) and LPP (bottom). Note that these were adjusted in the same manner as described for Fig. 3.2D. **E.** Within-subject differences in LEP amplitude between cued and uncued condition, with mean difference and 95% CIs. **F.** Within-subject differences in LPP amplitude between cued and uncued condition, with mean difference and 95% CIs.

3.4.2 Auditory N1

A 2 x 2 repeated measures ANOVA was conducted to assess the main effects of *cueing* (i.e., cued vs. uncued) and *probability* (i.e., 50% vs. 100%), as well as their interaction, on auditory N1 amplitudes in the motor-corrected waveforms (i.e., *motor-stimulus* minus equivalent *motor* conditions). Descriptive statistics relating to the motor-corrected N1 component amplitudes are presented in Table A2.3, while results of the ANOVA are reported in Table A2.6 (see Appendix 2). The ANOVA revealed a statistically significant main effect for *cueing*, $F(1, 63) = 9.671$, $p = .003$, $\eta_p^2 = .133$, $BF_{10} = 4.27E+00$ (see Fig. 3.4). In particular, N1 amplitudes in the *cued* conditions ($M = -3.50$, $SD = 2.38$) were found to be smaller (i.e., less negative) than those in the *uncued* conditions ($M = -4.11$, $SD = 2.22$). In contrast, the main effect of *probability* was not found to be statistically significant, $F(1, 63) = 0.01$, $p = .904$, $\eta_p^2 = .000$, $BF_{10} = 1.38E-01$. That is, N1 amplitudes in the 100% probability conditions ($M = -3.82$, $SD = 2.43$) did not differ significantly from those in the 50% probability conditions ($M = -3.79$, $SD = 2.21$). Similarly, the interaction between *cueing* and *probability* was not statistically significant, $F(1, 63) = 0.05$, $p = .821$, $\eta_p^2 = .000$, $BF_{10} = 1.90E-01$.

Fig. 3.4. Motor-corrected N1 analyses



A. Motor-corrected auditory evoked potentials (top), representing pooled mean amplitudes at Fz, FCz and Cz by condition, as well as 95% CIs. Difference between collapsed cued and uncued conditions (bottom), demonstrating sustained attenuation of cued conditions between approximately 100 ms and 200 ms post-stimulus **B.** Within-subject contrasts of N1 amplitude with mean difference and 95% CIs, as well as *p*-values representing the results of paired samples Student's t-tests. **C.** Topographic voltage maps for N1 components with corresponding condition labels and legend for panels A, B and D. **D.** Mean voltages and 95% CIs for N1 amplitudes by condition, as well as results reflecting the main effect of cueing on N1 amplitude.

3.4.2.1 Power Analyses

Post hoc power analyses explored the power (1- β) of the sample (*N* = 64) to assess small, medium and large effect sizes, according to standardised reporting conventions (Cohen, 1988). The sample was found to be sufficient to detect small ($\eta_p^2 = .01$), medium ($\eta_p^2 = .06$) and large ($\eta_p^2 = .14$) two-level repeated measures main effects with powers of .354, .978, and < .999, respectively.

3.5 Discussion

This investigation explored the influence of action-effect contingency on motor preparation for stimulus-driven and volitional action, as well as the processing of resultant stimuli. In addition to replicating several recent findings, we observed novel sensorimotor effects relating to both the generation of movement and stimulus processing. While our findings reflect involvement of action-effect contingency in motor preparation (i.e., reflected in RP amplitude), no such influence was apparent with respect to primary cortical response (i.e., as indicated by N1 amplitude). Contrary to our hypotheses, the influence of action-effect contingency was not found to differ between stimulus-driven and volitional action for either RP or N1 amplitudes. However, significant differences were observed in lateralised parieto-occipital activity that was observed at the time of enactment and shortly afterwards. In the following, we present a summary of these findings and synthesis with existing literature that serves to highlight the potential role of attention in distinct sensorimotor processes associated with volitional and stimulus-driven movement.

With respect to motor preparation, the amplitude of the late RP was found to be significantly larger when the probability of eliciting a tone was higher (i.e., *100%* compared with *50%*). This was consistent with recent evidence demonstrating that RP amplitude is influenced by action-effect contingency (Reznik et al., 2018; Vercillo et al., 2018; Wen et al.,

2018) and with theoretical frameworks emphasising the role of prediction in motor preparation (James, 1890; Wolpert et al., 1995). Although larger amplitudes were also observed for late RPs in stimulus-driven action (i.e., *cued* compared with *uncued*), caution is advised with respect to the interpretation of this effect. This is because separation of *cued* and *uncued* trials into different blocks meant that differences in the ERP associated with each form of action (i.e., post-stimulus) may have had differing effects on the baseline correction of subsequent trials (see Fig. A2.1). Findings demonstrated no significant influence of action-effect contingency on LRP amplitude. An interaction was also not observed between *cueing* and *probability* for either RP or LRP amplitude, with the associated Bayes Factors indicating substantial evidence in favour of a null effect. Contrary to hypotheses, these finding suggests that action-effect contingency may influence motor preparation for stimulus-driven and volitional action to similar degrees.

Exploratory analyses revealed lateralised activity in parieto-occipital regions at the moment of enactment (i.e., LEP) and shortly following (i.e., LPP), with relative positivity observed contralateral to the effector. To our knowledge, this is the first time that these components have been described and further investigation is needed to examine their specific functional properties. A tentative interpretation is nevertheless supported, based on experimental factors and shared characteristics with more established components. The N2pc is one such component that, like the LEP and LPP, involves lateralised potential over parieto-occipital regions. The N2pc, which was first described by Luck and Hillyard (1994), is observed over the hemisphere contralateral to subjects of covert visual attention. Evidence suggests that it reflects selective attentional mechanisms relating to the focus of one's spatial attention (Kiss et al., 2008). The Pd is another lateralised component that is maximal at similar scalp locations to the N2pc (Hickey et al., 2009). In contrast to the N2pc, which involves contralateral negativity reflecting enhancement of visual attention, the Pd involves contralateral *positivity* reflecting the *suppression* of visual attention (Hickey et al., 2009). Interestingly, a tactile equivalent to the visual N2pc has recently been described. This component, the N2cc, occurs at sites that are anterior to those used to examine the N2pc and has received growing support as an electrophysiological correlate to selective tactile attention since its discovery by Katus et al. (2014). If the N2cc has an analogous contralateral positivity that reflects suppression of tactile attention, as the Pd is to the N2pc, its topography may resemble that observed for the LEP.

Several lines of evidence indicate that the LEP may represent attentional processes that are directly involved in motor control. Significantly, the Pd has been found to reflect mechanisms that facilitate the termination of selective visuospatial attention (Sawaki et al., 2012). If the LEP is supported as an equivalent tactile component, it may therefore represent the withdrawal of tactile pre-motor attention involved in the generation of movement. That LEP amplitude was larger for stimulus-driven (i.e., *cued*) than volitional (i.e., *uncued*) action may reflect heightened motor attention during the cued task, which required that participants time their button press to coincide with passing stimulus lines. Such heightened motor attention during stimulus-driven action is consistent with evidence of increased corticospinal excitability in response to cues that have previously been paired with motor action (Tran et al., 2019).

At a theoretical level, our findings are consistent with the pre-motor account by Rizzolatti et al. (1987), which postulates that covert spatial orienting occurs prior to movement through activation of cortical circuits involved in motor preparation. This account has been supported by evidence that the speed of a saccade to a target stimulus is impaired following preparation of an alternate saccade, and that the level of inhibition increases as a function of distance between primed and target locations (Rizzolatti et al., 1987). It is proposed that this delay reflects the time taken to countervail prior orienting of attention before replacement with alternative oculomotor programmes. Research has also demonstrated that motor preparation enhances processing of stimulus features and spatial dimensions that are relevant to planned action (Craighero et al., 1999; Fagioli et al., 2007), providing further evidence that action planning influences attentional processes. In accordance with these findings, the LEP may instantiate termination of this selective attention at the moment of enactment.

While further investigation is needed, there are several indications that the LPP may also represent mechanisms involved in attentional suppression. Foremost, the topography of the LPP closely resembled that of the Pd (i.e., maximal effect when taken as the difference between PO7 and PO8). Research has demonstrated that the Pd may be elicited in response to the involuntary capture of attention (Sawaki & Luck, 2013). The timing of the LPP, which approximated that of the N1, may therefore reflect a role in the suppression of spatial attention to sensory outcomes of movement that have occurred during completion of each trial. In light of the fact that LPP amplitude was significantly larger for *cued* than *uncued* action, with no apparent lateralised activity in *uncued* conditions, this notion is also consistent with results pertaining to the auditory N1. That is, findings from the present investigation replicated recent research (Harrison et al., 2021) demonstrating a suppressed sensory response to stimulus-driven action (i.e., *cued* versus *uncued*). Significantly, a consistent level of suppression was observed between peaks of the N1 and P2 components in a manner reminiscent of the Nd wave generated by selective attention (see Hillyard et al., 1973). Taken together, these findings may therefore reflect multimodal attentional suppression of self-generated sensations for stimulus-driven action compared with volitional movement.

Within the active inference literature, it has been proposed that attention is used to weight sensory information in proportion to its assumed precision, serving as a form of gain control to prioritise among competing information channels (Feldman & Friston, 2010; Friston, 2009). Through this mechanism, attention may be diverted to rich sources of information and scaled according to the level of detail one intends to extract from a subject. According to this account, the allocation of attention during motor activity represents the optimal weighting of prediction error on proprioceptive channels associated with intended movement (Brown et al., 2011). In accordance with this interpretation, research suggests that corticospinal excitability during motor preparation is specific to effector muscle tracts (Mars et al., 2007) and shaped by contextual factors (Bestmann et al., 2008). The present findings may suggest that attention is suppressed with regard to the sensory consequences of stimulus-driven action, relative to those resulting from volitional movement. However, future research is needed to distinguish the apparent role of attention from other factors influencing motor coordination, such as associations between external stimuli that occur in synchrony with action (see Moeller & Pfister, 2022).

Results from the present investigation also hold significance for understanding mechanisms involved in sensory attenuation. This includes the potential role of attention, which previous literature has highlighted as a potential confound in research exploring the phenomenon (Hughes et al., 2013b). In addition to aforementioned evidence that attention is implicated in the execution of motor activity, it has long been known to influence the magnitude of neurophysiological responses to stimuli. For example, increased cortical activation has been observed when attention is focused on the ear to which sound stimuli are presented (Hillyard et al., 1973) and in response to target tone frequencies compared with distractors (Okamoto et al., 2007). Attention-mediated enhancement of cortical responsivity is believed to optimise sensory processing based on task-relevance (Näätänen & Michie, 1979), reflecting the allocation of attention to prioritised informational sources (Treisman & Gormican, 1988). For this reason, it has been posited that the phenomenon of sensory attenuation may reflect diversion of attention to effector muscles and away from resulting sensations (e.g., Horváth et al., 2012).

Crucially, action-effect contingency was not found to affect N1 amplitude and the associated Bayes Factor indicated substantial evidence in favour of a null effect. This finding suggests that one's neurophysiological response to self-generated stimuli is not affected by action-effect prediction. Significantly, this result is in contrast to the theorised operation of IFMs and other models positing suppression of anticipated sensations within primary sensory cortices. In a similar design to the present study, Harrison et al. (2021) demonstrated that the N1 amplitude elicited by self-generated tones resulting from volitional (i.e., *uncued*) action did not differ from that of externally-generated tones when these were made predictable in time. Evidence of a reduced neurophysiological response to tones that are produced by *cued* action might suggest that the phenomenon of sensory attenuation is specific to stimulus-driven movement. Findings from the present investigation may therefore suggest that sensory attenuation reflects attentional factors involved in the generation of movement and processing of subsequent sensations, rather than action-effect predictions within the internal forward model. Taken together, our results may support an account of sensory attenuation that emphasises the role of suppressive attentional mechanisms and specificity to sensations resulting from stimulus-driven action.

3.6 Conclusion

Findings from the present investigation suggest that, despite an apparent role in motor preparation, action-effect contingency does not influence primary cortical response to resultant stimuli. Larger RP amplitudes were observed prior to action that was associated with greater likelihood of eliciting a stimulus, including for both stimulus-driven (i.e., *cued*) and volitional (i.e., *uncued*) action. In contrast, the probability of a resulting stimulus was not found to influence the amplitude of the auditory N1 component. This is contrary to the central tenets of IFM-based models of sensory attenuation, which propose that motor commands are used to suppress self-generated sensations based on action-effect predictions.

Findings of an exploratory analysis revealed lateralised parieto-occipital activity at the time of enactment and shortly following (i.e., the LEP and LPP), which was larger for stimulus-driven than volitional action. Although further research is needed, we propose that the LEP may represent the termination of motor attention and the LPP reflects the suppression of attentional capture by resultant stimuli. Both components were found to be larger for stimulus-driven action compared with volitional action. The proposed suppressive attentional effect of the LPP is therefore consistent with reduced N1 amplitudes to sounds produced through stimulus-driven action, compared with those resulting from volitional movement.

Overall, our results suggest that sensory processing may be influenced by the nature of motor activity that has generated a stimulus though not the likelihood of resulting sensations. These findings may warrant a review of theoretical frameworks used to account for the phenomenon of sensory attenuation. We propose that the effect of sensory attenuation may differ with respect to volitional and stimulus-driven action, and is supported, at least in part, by differences in selective attention.

4. Action-effect prediction in sensory attenuation and error monitoring: Distinguishing stimulus-driven and volitional movement

Submitted for publication:[2]

Harrison, A. W., Christensen, B. K., & Whitford, T. J. (under review). *Action-effect prediction in sensory attenuation and error monitoring: distinguishing stimulus-driven and volitional movement*.

4.1 Abstract

While volitional movement is believed to be guided by action-effect predictions, these are thought to be less influential with respect to stimulus-driven movement. We compared the effects of predictability on auditory evoked responses to tones that were produced according to participants' (*N* = 61) own timing (i.e., volitionally) and in response to simple visual cues (i.e., stimulus-driven). N2b component amplitudes reflected error monitoring for sound resulting from volitional action, which was absent with respect to stimulus-driven movement. We also explored the sensory attenuation phenomenon, comparing evoked responses to stimuli produced by each form of action with those of externally-generated tones. When controlling for temporal predictability, N1 amplitudes elicited by externally-generated stimuli did not differ from those elicited by volitional or stimulus-driven movement. Reduced P2 amplitudes were observed in response to both volitional and stimulus-driven motor activity, supporting the role of attentional influences in the phenomenon of sensory attenuation.

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[2] This study has been posted as a preprint:
Harrison, A. W., Christensen, B. K., & Whitford, T. J. (2022). Action-effect prediction in sensory attenuation and error monitoring: distinguishing stimulus-driven and volitional movement. *PsyArXiv*. https://doi.org/10.31234/osf.io/t2bwk

4.2 Introduction

The term ‘sensory attenuation’ has been used to describe an observed reduction in the subjective intensity and neurophysiological response to stimuli when these are self-generated, compared with those produced externally (e.g., Blakemore et al., 1998; Schafer & Marcus, 1973). This phenomenon is thought to support the prioritisation of externally-generated sensations by suppressing the tides of sensory information associated with an organism’s own motor activities while it navigates through its surrounds (see Crapse & Sommer, 2008). Sensory attenuation is believed to be adaptive because, although representation of externally-generated events relies on information arriving through sensory channels, self-generated stimuli may be predicted based on the motor-activities through which they are produced. This notion has contributed to theoretical frameworks suggesting that self-generated sensations are suppressed *based on* predictions associated with eliciting motor commands (see Wolpert, 1997). Such accounts include the influential ‘internal forward model’ of motor control (IFM; Miall & Wolpert, 1996; Wolpert et al., 1995). According to the IFM, duplicates of motor commands (i.e. 'efference copies'; von Holst & Mittelstaedt, 1950) are transmitted to sensory cortices and activate representations of the anticipated consequences to movement (i.e., 'corollary discharge'; Sperry, 1950). Information arriving through afferent channels are believed to then be compared with these predictions, facilitating suppression of sensations that are anticipated on the basis of the eliciting motor command (Miall & Wolpert, 1996; Wolpert et al., 1995).

In addition to prioritising sensations that result from externally-generated events, computational mechanisms within the IFM are believed to facilitate the selection and enactment of movement based on its predicted outcomes (Wolpert et al., 1995). According to this account, dynamic control is supported through the detection of discrepancies between one’s predicted sensations and those arising in response to movement (Miall & Wolpert, 1996). Such discrepancy is represented within this system by residual sensory afference (i.e., the portion of one’s sensory experience that remains following removal of predictable self-generated sensations). The notion that action-effect predictions guide movement has been a central tenet to several other influential theories of motor control, including classical ideomotor theory (James, 1890; see review by Shin et al., 2010) and more contemporary perspectives within the active inference literature (Friston, 2009; Friston et al., 2010).

While action-effect prediction is believed to be central to the initiation and control of some forms of movement, it is considered to be less influential with regard to others. Previous research has distinguished between movement that is generated on the basis of action-effect associations (i.e., selection of a motor action based on its intended effects) from that which involves stimulus-response associations (i.e., movement in reaction to an external stimulus; Neumann, 1984). Evidence suggests that motor activity may be initiated by either form of learned association, depending on whether it is volitional (i.e., internally-cued) or stimulus-driven (i.e., externally-cued; Herwig et al., 2007). In this manner, volitional movement is believed to be guided by its anticipated sensory consequences (Herwig et al., 2007; Pfister et al., 2011) while stimulus-driven movement may operate as a form of prepared reflex with less regard for its specific effects (see Hommel, 2000). In addition to experimental findings (Herwig et al., 2007), the distinction between volitional and stimulus-driven movement has been supported by evidence indicating differing neuroanatomical substrates (see Fried et al., 2017). If stimulus-driven movement is not initiated on the basis of action-effect predictions or guided by subsequent comparison with resulting sensations, the IFM does not appear necessary to its operation. Down-weighting of action-effect prediction in the generation of such movement may leave other proposed functions of the IFM unfulfilled, however, including prediction-based suppression of self-generated sensations. Suppression of sensations resulting from stimulus-driven action may therefore involve alternate mechanisms to those supported by action-effect prediction within the IFM.

A distinction between volitional and stimulus-driven action has particular relevance in the context of research that has investigated sensory attenuation through examination of the auditory N1 component (e.g., Han et al., 2021; Han et al., 2022; Schafer & Marcus, 1973; Schröger et al., 2015). The N1 is a large negative component of the auditory evoked potential that occurs between 75 ms and 125 ms after stimulus onset, with subcomponents originating in the supratemporal plane, superior temporal gyrus, and regions within the motor cortex and/or cingulate gyrus (see Giard et al., 1994; Näätänen & Picton, 1987). It is believed to provide a reliable indicator of neurophysiological responses within the primary auditory cortex (see Zouridakis et al., 1998) and has been used extensively in research exploring sensory attenuation (e.g., Schafer & Marcus, 1973; Schröger et al., 2015). In a series of experiments, Harrison et al. (2021) compared the amplitude of N1 components elicited by stimuli that were generated according to participants' own timing (i.e., volitional) and those produced in response to simple visual cues (i.e., stimulus-driven). Results supported an action cueing effect, whereby reduced N1 amplitudes were observed for sounds that were elicited by stimulus-driven action compared with those resulting from volitional movement (Harrison et al., 2021).

The effect of action cueing is particularly important when taken in conjunction with that of temporal predictability, which has been shown separately to influence N1 amplitudes (e.g., Lange, 2009; Weiskrantz et al., 1971) and represents a potential confound in much of the sensory attenuation literature (see Hughes et al., 2013b). Significantly, the amplitude of N1 components elicited by sound resulting from volitional action has been found not to differ from that of externally-generated stimuli when these are made predictable in time (Harrison et al., 2021). In contrast, the amplitude of N1 components resulting from sounds produced through stimulus-driven action have been found to be reduced relative to temporally-predictable externally-generated sounds (Harrison et al., 2021). These findings highlight the importance of controlling for effects relating to temporal predictability in research examining sensory attenuation, and differentiating sensory effects associated with volitional and stimulus-driven action.

Evidence that the auditory N1 is not sensitive to the likelihood of action eliciting sound stimuli (i.e., action-effect contingency) presents another significant challenge to research that has explored IFM-based suppression through examination of this component. Findings from another recent investigation suggest that the amplitude of N1 components elicited by stimuli resulting from volitional and stimulus-driven action are not influenced by action-effect contingency (Harrison, Hughes, et al., 2022). This suggests that suppression of the N1 response to sounds resulting from stimulus-driven action, compared with those produced by either volitional action or externally-generated events, may not be attributable to effects associated with IFM operation. Instead, Harrison, Hughes, et al. (2022) provide tentative evidence that this phenomenon may reflect the outcome of selective attentional mechanisms. Overall, these findings indicate that N1 amplitude is sensitive to the form of action that has elicited stimuli (i.e., whether volitional or stimulus-driven) and that this effect may contribute to differences between self- and externally generated sensations in a manner not associated with motor-based predictions.

While most previous studies of sensory attenuation and other IFM mechanisms have focused on the N1 component, several additional components of the auditory evoked response may provide useful information to understanding these sensorimotor phenomena. This includes the P2 and N2b components in particular. The P2 manifests as a centralised positive component that occurs between 150 ms and 250 ms after stimulus onset (see Crowley & Colrain, 2004). While the functional significance of the P2 remains relatively poorly understood, several lines of evidence have identified effects involving attentional control. This has included the ‘processing negativity’, whereby heighted attention to a stimulus contributes to a simultaneous enhancement of its resulting N1 amplitude and a reduction in P2 amplitude (Hillyard et al., 1973; Näätänen et al., 1978). Significantly, an effect consistent with processing negativity has been observed for stimuli produced by volitional action compared with those produced by stimulus-driven action (Harrison, Hughes, et al., 2022).

Attention-related suppression of the P2 has also been observed independently of N1 effects, including with respect to non-target stimuli in auditory oddball tasks when compared with those elicited by identical stimuli when these are not task-relevant (García-Larrea et al., 1992; Novak et al., 1992). These findings have led to the suggestion that reduced P2 amplitude reflects enhanced attentional control during auditory discrimination tasks (Crowley & Colrain, 2004), including processes involved in its termination (García-Larrea et al., 1992). Involvement of the P2 in attentional control is also consistent with evidence demonstrating a linear increase in its amplitude with age, corresponding to an age-related decline in capacity to resist attentional capture (García-Larrea et al., 1992). It has also been noted (see Crowley & Colrain, 2004) that the frontal sites at which these P2 effects are most prominent overlay brain regions involved in protecting against interference by irrelevant stimuli (Dempster, 1992) and those most affected by aging (Pfefferbaum et al., 1998). Examination of P2 components elicited by self- and externally-generated stimuli may therefore serve to further evaluate recent indications regarding involvement of attentional processes in the sensory attenuation phenomenon.

The N2b is a negative frontocentral component that occurs between 200 ms and 350 ms following stimulus onset (see Folstein & Van Petten, 2008). Larger N2b amplitude has been observed in response to stimuli presented during activities with increased cognitive load, including response inhibition (Bruin & Wijers, 2002) and covert counting tasks (Harrison et al., 2021; Mertens & Polich, 1997). Significantly, the N2b has also been implicated in error monitoring processes. In an experiment by Ferdinand et al. (2008), participants were required to respond to each letter in a sequence with button presses involving different fingers. A repeating sequence was occasionally interrupted by deviant trials, in which the presented letter required a response with an alternate finger. Ferdinand et al. (2008) observed increased N2b amplitudes to self-generated stimuli that deviated from the sequence, with this effect increasing over the course of the experiment. On this basis, it was proposed that deviant events were perceived as errors committed by the participant and reflected in the N2b response. As the IFM framework and other theories of motor control suggest that predictions regarding the outcome of movement are inherent to its production, examination of N2b effects is also warranted.

The present study therefore aimed to compare the influence of stimulus predictability on neurophysiological responses to self- and externally-generated stimuli. We sought to differentiate sensorimotor processes in stimulus-driven and volitional action, and to assess and control for the effect of temporal predictability. These aims were achieved through comparison of the event-related potentials (ERPs) elicited by self- and externally-generated sound that differed with respect to these factors. Self-generated tones were produced according to participants' own timing (i.e., volitionally) or in response to simple visual cues (i.e., stimulus-driven). In the case of externally-generated tones, the absence or presence of these visual cues supported an assessment of the effects of temporal predictability and its control in the comparison between self- and externally-generated stimuli (see Fig. 4.1). To facilitate comparison of effects relating to action-effect prediction, two variants of each condition presented sequences of either a single tone type or two different frequencies.

4.3 Method

4.3.1 Participants

Sixty-one healthy participants (42 females), aged between 18 and 50 years (*M* = 22.07, *Mdn* = 20.27, *SD* = 5.81), took part in exchange for credit towards an undergraduate psychology unit at the University of New South Wales (UNSW). The study was approved by the UNSW Human Research Ethic Advisory Panel and recruitment was undertaken through the university's electronic recruitment system (SONA).

4.3.2 Material and Design

Participants were seated facing a BenQ XL2420T computer monitor (24-inch, 1920 × 1080 resolution screen) at a distance of approximately 60 cm. They were fitted with an EEG recording cap, which was equipped with a BioSemi ActiveTwo system containing 64 Ag/Cl active electrodes. These were positioned according to the extended 10:20 layout. Each participant was also fitted with electrodes below the left eye, on their nose, adjacent to the outer canthus of each eye, and on their left and right mastoids. Participants wore Sennheiser HD201 headphones, placed over the recording cap and electrodes. Grounding was provided by the CMS and DRL cap electrodes while data acquisition was undertaken with a sampling rate of 2048 Hz. In each condition, participants were asked to fix their gaze on a vertical red (fixation) line at the centre of the screen. This line was one pixel wide and approximately six centimetres long (i.e., corresponding to a visual angle of approximately 5.4°).

In *uncued* conditions, a sequence of randomly-spaced white line fragments were presented across five adjacent rows that collectively spanned the height of the fixation line (see Fig. 4.1B). The line fragments appeared on the right of the screen and moved leftward at a pace of approximately 3°/s. In the *motor-auditory* and *motor* variants of the *uncued* condition, participants were instructed to press a keyboard button repeatedly. They were asked to make the timing of their button presses unpredictable to an observer, and to aim for approximately two to four seconds between each press. Brief reminders were displayed above the fixation line from 400 ms to 800 ms post-stimulus following trials in which participants had pressed with less than two seconds between their button presses. The reminder, which asked participants to "slow down", was infrequently required.

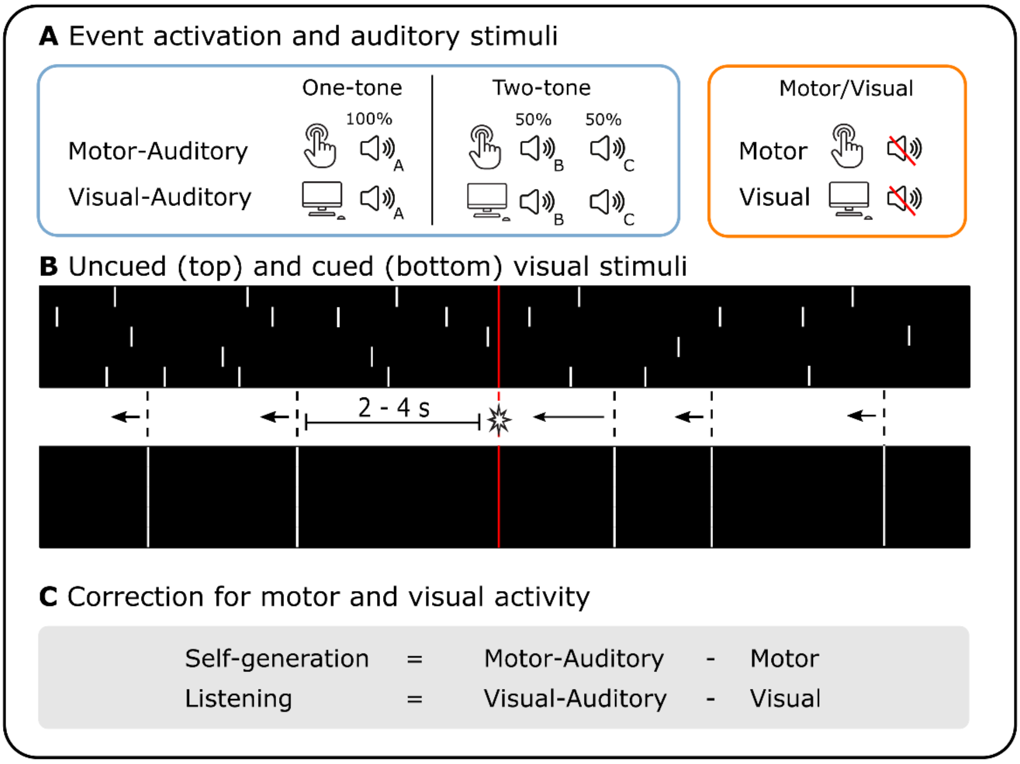
In the *uncued motor-auditory* condition, each button press resulted in delivery of a pure tone (85 dB, SPL/A-weighted, 10 ms ramp, 100 ms duration) via participant headphones. In the *one-tone* variant of this condition, all tones were of the same frequency. These could be either *low*, *medium* or *high* pitch tones, corresponding to 500 Hz, 1000 Hz and 1500 Hz respectively. In a *two-tone* variant, each button press elicited one of two different tones. The total number of each tone type was balanced within blocks and presented in randomised order. Allocation of the three tone frequencies to the *one-tone* and *two-tone* variants was counterbalanced across participants. In the *motor* variant of the *uncued* condition, silent audio tracks were triggered to mark each button press. Latency of audio track delivery (i.e., both tones and silent tracks) was reduced with the assistance of an AudioFile Stimulus Processor (Cambridge Research Systems).

Participants observed passively in the *visual-auditory* and *visual* variants of the *uncued* condition. In the *one-tone* variant of the *visual-auditory* condition, a sequence of tones with a single frequency was presented to participants. In the *two-tone* variant, a sequence of two different tone frequencies were again presented. The allocation of tone frequencies to each condition, and their order within *two-tone* sequences, was the same as for the *uncued motor-auditory* conditions. The timing of their presentation was also matched to the timing of participants' button presses in the preceding *uncued motor-auditory* condition. In *visual* conditions, the timing of silent audio tracks was determined based on this approach.

In *cued* conditions, vertical white (stimulus) lines appeared on the right of the screen and moved leftward at a constant rate of approximately 3°/s. These lines were one pixel wide and approximately six centimetres long (i.e., equal dimensions to the fixation line; see Fig. 4.1B). In the *motor-auditory* and *motor* variants of the *cued* condition, participants were instructed to press the keyboard button at the precise moment that each stimulus line intersected with the fixation line. The spacing of the lines, and therefore the timing of events, was based on the spacing of participants' button presses in the preceding *uncued motor-auditory* or *uncued motor* block (i.e., the most recently presented). Button presses in the *cued motor-auditory* condition elicited the same auditory stimuli as described for the *uncued motor-auditory* and *uncued visual-auditory* conditions, with different blocks presenting *one-tone* and *two-tone* sequences. Button presses again triggered delivery of a silent audio track to mark events in the *cued motor* condition. Participants were instructed to passively observe in the *cued visual-auditory* and *cued visual* conditions. In the *cued visual-auditory* condition, tones were presented at the precise moment that each stimulus line intersected with the fixation line. Auditory stimuli were the same as described for other conditions, with *one-tone* and *two-tone* block varieties. Silent audio tracks were used to mark these events in the *cued visual* condition.

Participants completed a single block of each of the twelve experimental conditions. Each block involved a total of 70 trials. The order of blocks was pseudorandomised, such that the *uncued motor-auditory* and *uncued motor* conditions were presented in the first or seventh block. The allocation of these conditions to each block was counterbalanced across participants, while the order of the 10 remaining conditions was randomised for each participant.

Fig. 4.1. Protocol schematic and visual stimuli



A. In *motor-auditory* and *motor* conditions, participants pressed a keyboard button to initiate events. These were initiated externally, by the computer, in the *visual-auditory* and *visual* conditions. Events involved presentation of a tone via participant headphones in the *motor-auditory* and *visual-auditory* conditions, while silent audio tracks were used to mark events in the *motor* and *visual* conditions. In *one-tone* variants of the *motor-auditory* and *visual-auditory* conditions, all tones were of a single frequency. A balanced and randomised sequence two different tone frequencies were presented in the *two-tone* variants. **B.** In *uncued* conditions, vertical line fragments were randomly distributed across five adjacent rows and moved leftwards across the screen. In the *motor-auditory* and *motor* variant, participants were instructed to ignore these lines, keep their eyes fixed on a red fixation line and press a keyboard button once every two to four seconds approximately. The timing of events (i.e., inter-trial intervals) in the preceding *motor-auditory* condition provided the bases for timing in subsequent *visual-auditory* and *visual* conditions. In *cued* conditions, this timing was represented by longer vertical lines that moved from right to left across the screen. In *motor-auditory* and *motor* variants of the *cued* condition, participants were instructed to press the keyboard button to initiate events at the precise moment that each line intersected with the fixation line. Events were externally triggered at this precise in the *visual-auditory* and *visual* variants. **C.** *Motor-auditory* conditions were corrected for motor (and visual) activity by subtracting the equivalent *motor* condition (i.e., *uncued* and *cued*). Similarly, visual activity was removed from the *visual-auditory* conditions by subtracting the equivalent *visual* condition. Motor-corrected motor-auditory conditions are described as *self-generation,* while visual-corrected visual-auditory conditions are described as *listening.* Twelve experimental conditions were thereby used to develop eight analysis conditions, including *one-tone* and *two-tone* variants of the *uncued self-generation, cued self-generation, uncued listening* and *cued listening* conditions.

4.3.3 EEG Processing

EEG data were referenced to the nose electrode and processed offline in BrainVision Analyser (Version 2.2.0; Brain Products GmbH, Gilching, Germany). A 50-Hz notch filter and 0.1 Hz to 30 Hz zero phase shift Butterworth band-pass filter (half-amplitude, high-pass 12 dB/Oct and low-pass 48 dB/Oct slopes) were applied. Trials were segmented into 600 ms epochs, commencing 200 ms prior to each event. Recordings from the electrodes below participants' left eyes were used in conjunction with those at Fp1 to produce vertical electro-oculograms (EOGs). Horizontal EOGs were similarly constructed based on recordings at the electrodes that were placed adjacent to the outer canthus of each eye. EOGs were then used to correct eye movement artefacts using the method described by Miller et al. (1988), which is an extension to the approach by Gratton et al. (1983). Baseline correction was applied using average recordings in the 200 ms prior to each event. Epochs that were found to contain peak-to-peak amplitudes in excess of 200 µV were then excluded. Averaged waveforms were developed by condition and participant, based on the remaining epochs.

Activity associated with the auditory stimuli in *motor-auditory* and *visual-auditory* conditions was isolated by subtracting equivalent *motor* and *visual* waveforms. Twelve experimental conditions thereby supported calculation of eight analysis conditions, including *one-tone* and *two-tone* varieties for each task conditions, including *uncued self-generation, cued self-generation, uncued listening* and *cued listening.*

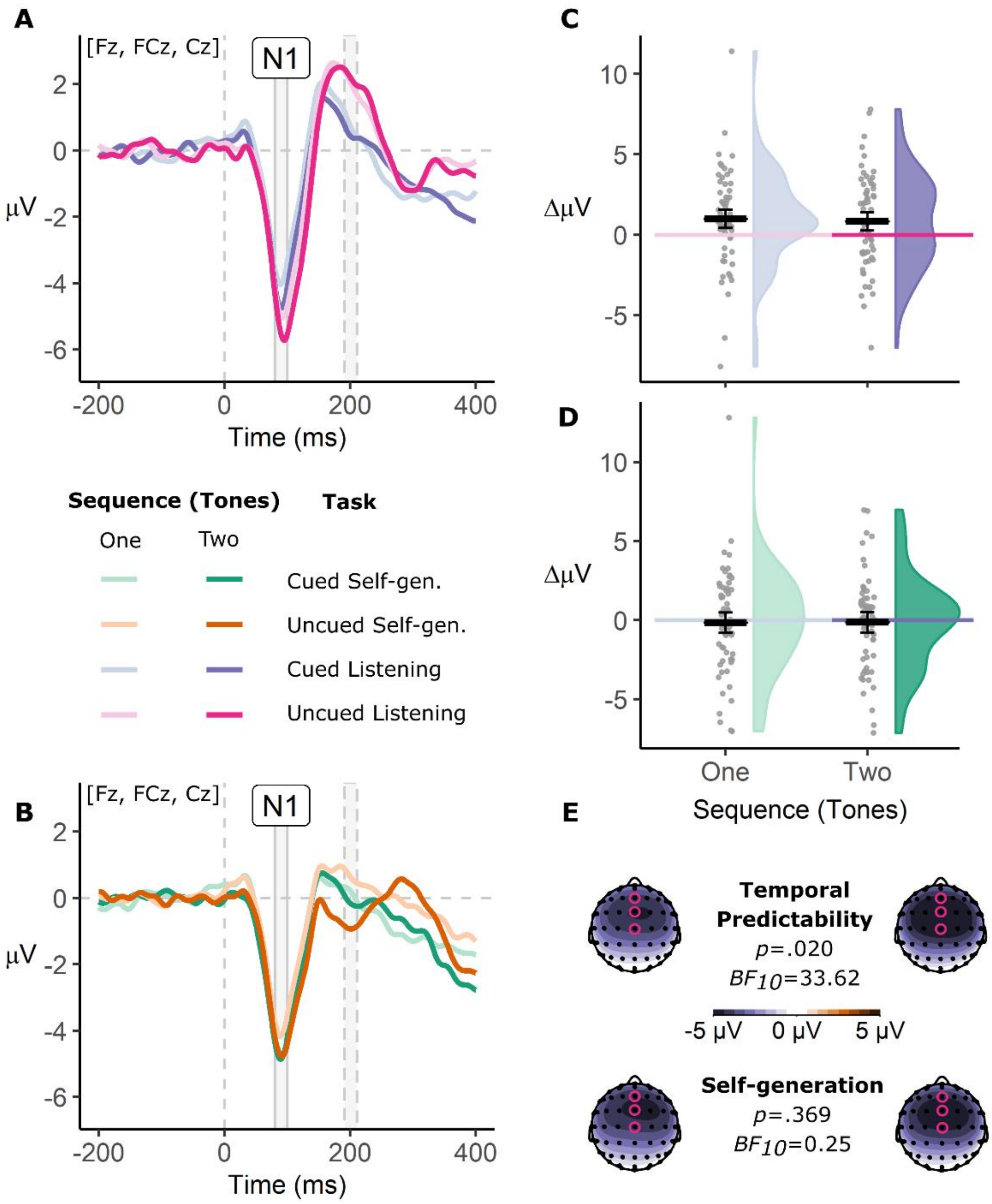
Consistent with previous analyses (e.g., Harrison et al., 2021), the N1 and N2b were analysed based on pooled recordings at Fz, FCz and Cz, while the P2 was analysed based on pooled recordings at FCz, Cz and CPz. Peak latencies of the N1 and P2 components were identified using the collapsed localizer method (see Luck & Gaspelin, 2017). This involved identifying component latency within a collapsed waveform that represented the average voltages across all participants and conditions. When defined as the most negative local minimum between 50 ms and 150 ms, the N1 was found to have occurred 90.3 ms post-auditory stimulus. The P2 was found to have occurred 161.1 ms after stimulus onset, when defined as the most positive local maximum between 40 ms and 170 ms post-auditory. Because a clear N2b component was only evident in the *two-tone uncued self-generation* condition (see Fig. 4.2), the grand-averaged waveform of this condition was used as the basis for determining its latency. When taken as the most negative local minimum between 150 ms and 300 ms post-auditory, the N2b peak was found to have occurred 200.7 ms post-auditory stimulus. An apparent P3 component was also observed in the *two-tone uncued self-generation* condition, with a latency of 279.3 ms when taken as the most positive local maximum between 250 ms and 350 ms.

4.4 Results

4.4.1 N1

A 2 x 4 repeated measures ANOVA was used to investigate the main effects of *sequence* (i.e., *one-tone* versus *two-tone*) and *task*, as well as their interaction, on N1 component amplitudes (see *Statistical Analyses)*. Planned comparisons involved three orthogonal contrasts of the *task* condition (i.e., *uncued self-generation, cued self-generation, uncued listening* and *cued listening)*, supporting investigation of the effects of *volition* ([3, -1, -1, -1]), *self-generation* ([0, 2, -1, -1]) and *temporal predictability* ([0, 0, -1, 1]). As these contrasts were both planned and orthogonal, their statistical significance was not corrected for multiple comparisons. Non-sphericity was identified by Mauchly's test (Mauchly, 1940) and corrected using the Greenhouse-Geisser method (Geisser & Greenhouse, 1958). The ANOVA revealed statistically significant main effects of both *sequence*, $F(0.86, 51.72) = 11.86$, $p = .001$, $\eta_p^2 = 0.17$, $BF_{10} = 9.18$, and *task*, $F(2.94, 176.56) = 2.91$, $p = .036$, $\eta_p^2 = 0.05$, $BF_{10} = 1.76$ (see Fig. 4.2). Planned comparisons indicated a significant effect of *temporal predictability* (i.e., contrasting *cued listening* and *uncued listening)*, $t(180) = 2.34$, $p = .020$, $d = 0.30$, $BF_{10} = 33.62$, such that *cued listening* exhibited a smaller (i.e., less negative) N1 amplitude than *uncued listening.* The effects of *volition* and *self-generation* were not found to be significant (see Table A3.3 for detail). Nor were interactions between the effect of *sequence* and each of the planned comparisons. This included the *temporal predictability* x *sequence* interaction, $t(240) = -0.32$, $p = .751$, $d = -0.04$, $BF_{10} = 0.11$, and the *self-generation* x *sequence interaction,* , $t(240) = -0.13$, $p = .896$, $d = -0.02$, $BF_{10} = 0.17$. In both cases, the associated Bayes factor indicated substantial evidence in favour of the null hypothesis (see Jeffreys, 1998).

Fig. 4.2. Analyses of N1 component amplitudes



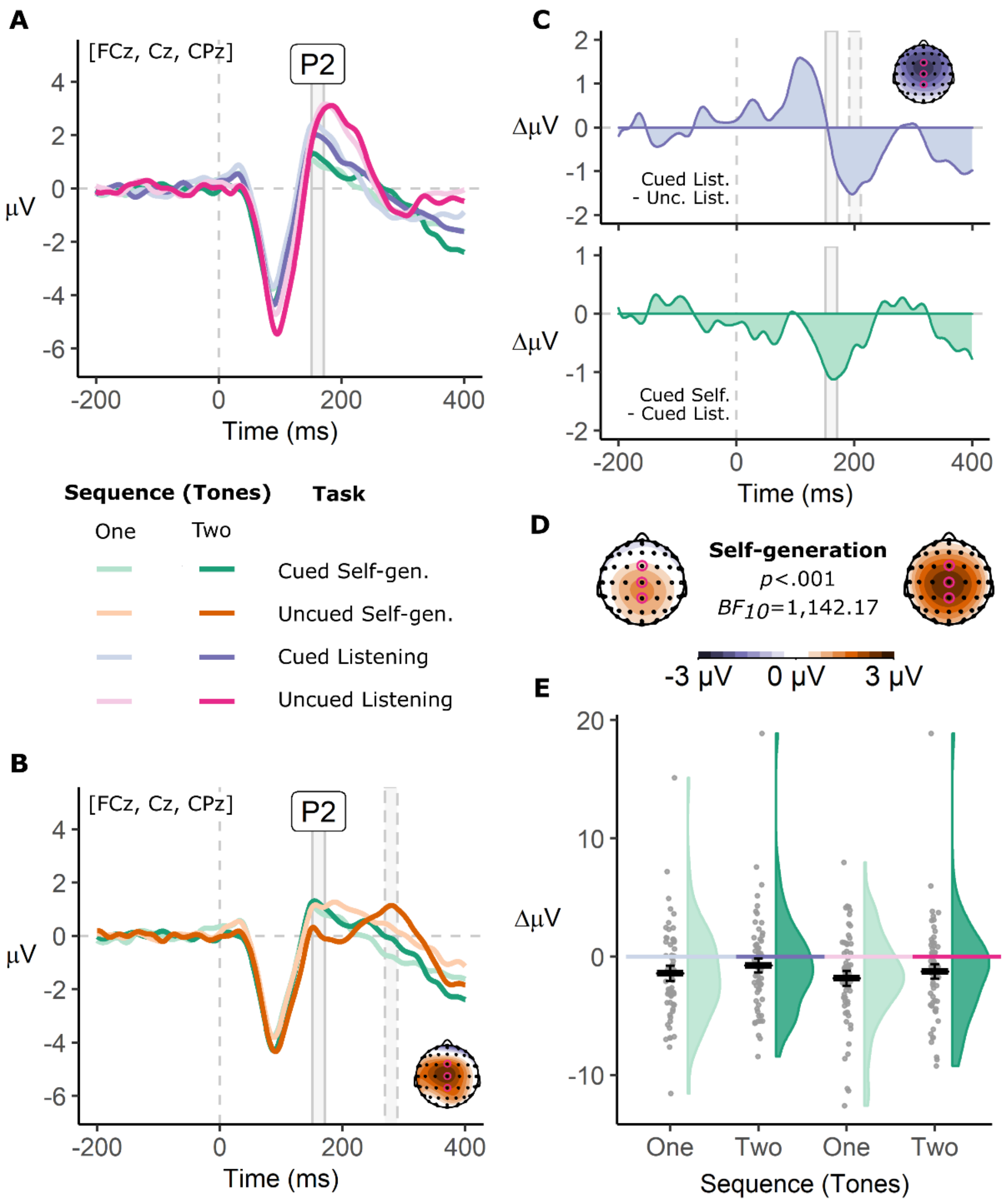
A-B. Pooled grand-averaged recordings at Fz, FCz and Cz, demonstrating mean amplitude for (A) *listening* conditions and (B) *self-generation* conditions, by *sequence* (i.e., *one-tone* and *two-tone*). Dotted rectangles mark N2b analysis window. **C-D.** Within-subject differences in mean N1 amplitude between (C) *cued listening* and *uncued listening* and (D) *cued self-generation* and *cued listening*, by *sequence* (i.e., *one-tone* and *two-tone*).

E. Statistical test outcomes relating to the effects of temporal predictability and self-generation. Accompanying topographic maps demonstrate the contrast in N1 distribution between the (top left) *cued listening* and (top right) *uncued listening* conditions, and between (bottom left) *cued self-generation* and combined (bottom right) *listening* conditions. Pink rings indicate analysis electrodes.

4.4.2 P2

Differences in P2 component amplitude were also investigated using a 2 x 4 repeated measures ANOVA. This was used to examine effects involving experimental *sequence* and *task*, as well as their interaction. Non-sphericity was again corrected using the Greenhouse-Geisser method (Geisser & Greenhouse, 1958). The ANOVA revealed a statistically significant effect of *task* on P2 amplitude, $F(2.22, 133.15) = 9.25$, $p < .001$, $\eta_p^2 = 0.13$, $BF_{10} =$ 334,906.58 (see Fig. 4.3). In contrast, non-significant effects were observed with respect to *sequence*, $F(0.77, 45.95) = 1.67$, $p = .201$, $\eta_p^2 = 0.03$, $BF_{10} = 0.23$, and the interaction between *task* and *sequence*, $F(2.30, 137.84) = 1.97$, $p = .120$, $\eta_p^2 = 0.03$, $BF_{10} = 0.07$. Planned comparisons revealed statistically significant effects of both *self-generation*, $t(180) = -3.57$, $p < .001$, $d = -0.46$, $BF_{10} = 1{,}142.17$, and *volition*, $t(180) = -2.09$, $p = .038$, $d = -0.31$, $BF_{10} =$ 1,223.77, on P2 amplitude. Significance of the *self-generation* effect suggested that the *cued self-generation* condition had a smaller (i.e., less positive) P2 amplitude than the *listening* conditions (i.e., *uncued listening* and *cued listening)*. The nature of the *volition* effect was such that the *uncued self-generation* condition exhibited a smaller P2 amplitude than the *cued self-generation* condition. Other planned comparisons and interactions with the effects of *sequence*, were not found to be statistically significant (see Table A3.3).

Fig. 4.3. Analyses of P2 component amplitudes



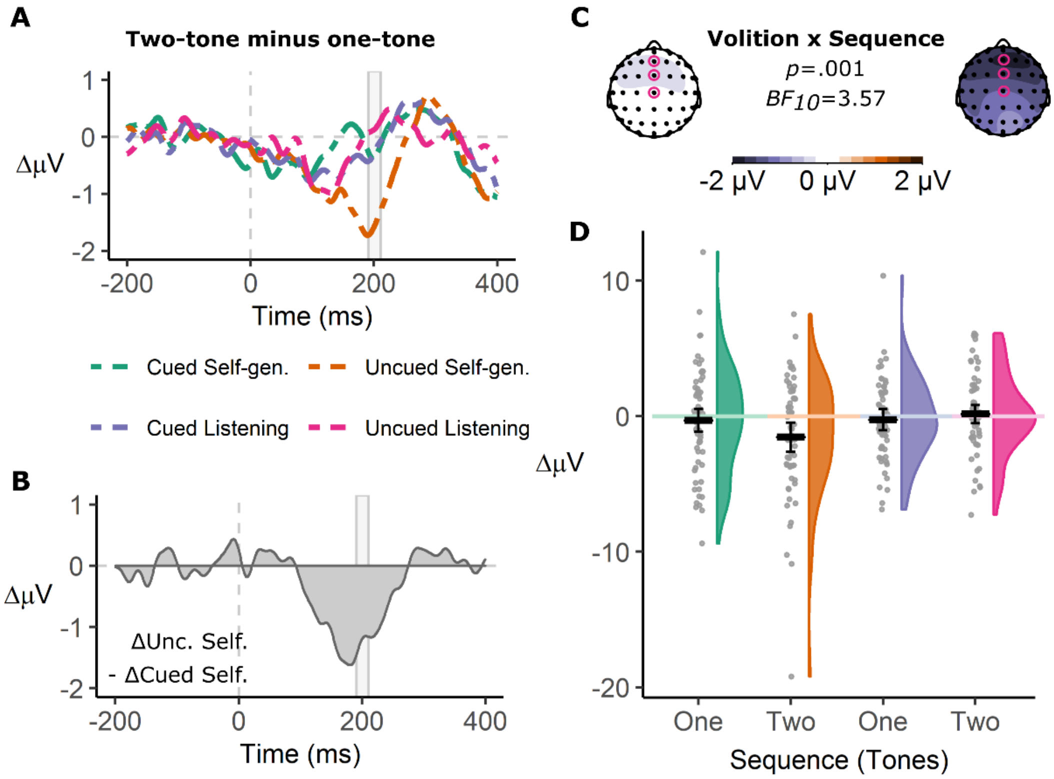
A-B. Pooled grand-averaged recordings at FCz, Cz and CPz, demonstrating mean amplitude for (A) *cued self-generation, cued listening* and *uncued listening* conditions and (B) all *self-generation* conditions, by *sequence* (i.e., *one-tone* and *two-tone*). Dotted rectangle and accompanying topographic map in (B) demonstrate the P3 component (279 ms post-stimulus) in the *two-tone uncued self-generation* condition. **C.** Difference waves, representing (top) *cued listening* minus *uncued listening,* and (bottom) *cued self-generation* minus *cued listening* (i.e., combined one-tone and two-tone variants). Difference waves are collapsed across sequence (i.e., combining one- and two-tone variants). Dotted rectangle and accompanying topographic voltage map demonstrate the distribution of difference waves at the N2b analysis window, appearing to reflect reduced latency and amplitude of the P2 in *cued listening* compared with *uncued listening*. **D.** Statistical test outcomes relating to the effect of self-generation and accompanying topographic maps, including (left) *cued self-generation* and (right) combined *listening* conditions. Pink rings indicate analysis electrodes. **E.** Within-subject differences in mean P2 amplitude, including *cued self-generation* minus *cued listening* and *uncued listening* conditions by *sequence* (i.e., *one-tone* and *two-tone*).

4.4.3 N2b

To investigate effects involving the N2b component, another 2 x 4 repeated measures ANOVA was conducted. This again supported examination of the main effects of *sequence* and *task*, as well as their interaction. Mauchly's test identified non-sphericity (Mauchly, 1940), which was again corrected using the Greenhouse-Geisser method (Geisser & Greenhouse, 1958). Results indicated a statistically significant effect of *task*, $F(2.46, 147.33) = 10.68$, $p < .001$, $\eta_p^2 = 0.15$, $BF_{10} = 4{,}336{,}194.87$. While the main effect of sequence was not significant, $F(0.80, 47.73) = 2.14$, $p = .149$, $\eta_p^2 = 0.03$, $BF_{10} = 0.26$, a statistically significant interaction was observed between *task* and *sequence*, $F(2.39, 143.18) = 4.71$, $p = .003$, $\eta_p^2 = 0.07$, $BF_{10} = 0.42$ (see Fig. 4.4). Planned comparisons revealed significant effects associated with *self-generation,* $t(180) = -2.41$, $p = .017$, $d = -0.31$, $BF_{10} = 1{,}254.35$, and *temporal predictability,* $t(180) = -2.23$, $p = .027$, $d = -0.29$, $BF_{10} = 6{,}692.37$. The effect of *self-generation* was such that the *cued self-generation* condition had larger (i.e., more negative)

N2b components compared with those of the *listening* conditions (i.e., *uncued listening* and *cued listening)*. The temporal predictably effect was such that larger N2b components were observed in the *cued self-generation* condition compared with the *uncued self-generation* condition. Interestingly, a significant interaction was also observed between *volition* and *sequence*, $t(240) = -3.28$, $p = 0.001$, $d = -0.49$, $BF_{10} = 3.57$. This interaction was such that the *two-tone* sequence resulted in larger N2b amplitudes than the *one-tone* sequence in the *uncued self-generation* condition, while this effect was not apparent with respect to the *cued self-generation* condition.

Fig. 4.4. Analyses of N2b component amplitudes



A. Difference waves representing *two-tone* minus *one-tone* variants by task condition, including *cued self-generation, uncued self-generation, cued listening* and *uncued listening* condition. **B.** Difference wave, representing differences in the effect of sequence (i.e., *two-tone* minus *one-tone*) between *cued self-generation* and *uncued self-*

generation conditions. **C.** Statistical test outcomes relating to the interaction between volition and sequence. Accompanying topographic maps represent the effect of sequence (i.e., *two-tone* minus *one-tone*) for (left) combined *cued self-generation, cued listening* and *uncued* listening, and (right) *uncued self-generation.* Pink rings indicate analysis electrodes. **D.** Within-subject differences in mean N2b amplitude by sequence (i.e., *two-tone* minus *one-tone*) for each task condition, including *cued self-generation, uncued self-generation, cued listening* and *uncued listening.*

4.4.4 Behavioural

Descriptive statistics relating to ITI are provided by condition in Table A3.4. A 3 x 4 repeated measures ANOVA was used to assess consistency in ITI across experimental conditions. Specifically, this examined differences based on the nature of *auditory stimuli* (i.e., motor/visual, one-tone and two-tone), *event activation* (i.e., self-generated versus external) and *visual stimuli* (i.e., uncued versus cued). Following correction for non-sphericity using the Greenhouse-Geisser method (Geisser & Greenhouse, 1958), results from the ANOVA identified non-significant effects with respect to each factor, including *auditory stimuli*, $F(1.96, 117.60) = 0.07$, $p = .930$, $\eta_p^2 = 0.00$, $BF_{10} = 0.02$, *event activation*, $F(0.84, 50.70) = 0.35$, $p = .554$, $\eta_p^2 = 0.01$, $BF_{10} = 0.10$, and *visual stimuli*, $F(0.94, 56.39) = 1.81$, $p = .184$, $\eta_p^2 = 0.03$, $BF_{10} = 0.32$. Interactions were also found to be non-significant (see Table A3.5 for detail). Overall, these results reflect relative consistency in ITI across experimental conditions.

4.4.5 Power Analyses

The power ($1 - \beta$) of the sample ($N = 61$) to assess small, medium, and large effect sizes, was explored through post hoc analyses. Based on standardised reporting conventions

(Cohen, 1988), the sample was sufficient to detect small ($\eta_p^2 = .01$), medium ($\eta_p^2 = .06$) and large ($\eta_p^2 = .14$) two-level repeated measures main effects with powers of .339, .973, and < .999, respectively. With regard to three-level main effects, the sample was found to achieve powers of .379, .993, and < .999, respectively.

4.5 Discussion

In the present investigation, we compared the effects of predictability on evoked responses to self- and externally-generated stimuli. The study was designed to evaluate and control for effects relating to differences in temporal predictability, serving to address prior methodological limitations in this regard. We also differentiated between stimulus-driven and volitional movement, given evidence demonstrating distinct neuroanatomical substrates and sensorimotor processing. Importantly, the study sought to provide an exploratory analysis of relevant components across the evoked response. In addition to the auditory N1, this included analyses of P2 and N2b component amplitudes.

Findings replicated previous research (e.g., Lange, 2009; Weiskrantz et al., 1971) in demonstrating reduced N1 amplitudes (i.e., relative positivity) to stimuli when these were made predictable in time (i.e., *cued listening* versus *uncued listening)*. The effect of *self-generation* was not found to be significant when controlling for *temporal predictability*, with N1 amplitudes in the *cued listening* condition not found to differ from those relating to self-generated stimuli in the *uncued self-generation* and *cued self-generation* conditions. The corresponding Bayes Factor suggests substantial evidence in favour of mean amplitudes not differing in this regard. This finding is in contrast with previous research that has identified differences between the amplitude of N1 components elicited by self- and externally-generated stimuli. In this manner, they provide further indication that such differences may in many instances be attributed to the inherent temporal predictability of self-generated sensations.

In contrast with recent findings (Harrison, Hughes, et al., 2022; Harrison et al., 2021), the effect of *volition* (i.e., contrasting *cued self-generation* with *uncued self-generation* and both *listening* conditions) was not found to be significant either. Although the reasons for this difference are not immediately apparent, it is noteworthy that the current study involved longer ITIs than in previous investigations. This was due to the inclusion of prompts, which reminded participants to slow down following trials with an ITI less than 2000 ms. Future research may therefore examine the potential that the effect of action cueing on N1 is moderated the interval between self-generated stimuli.

The effect of *sequence* (i.e., contrasting *one-tone* and *two-tone* variants of each condition) on N1 amplitude was significant, reflecting a reduced primary cortical response in series of trials involving only one tone frequency. However, the non-significant *sequence* x *self-generation* interaction suggested that N1 amplitudes were not differentially affected by tone frequency prediction for self- and externally-generated stimuli. This finding is consistent with evidence that N1 amplitude is not influenced by the likelihood of action eliciting a specific stimulus (Harrison, Hughes, et al., 2022), and is contrary to the attribution of reduced N1 amplitudes for self-generated stimuli to the effects of motor-based prediction. The *sequence* x *temporal predictability* interaction was also not found to be significant, suggesting that tone frequency prediction did not confer additional suppression to passively observed stimuli when these were made predictable in time. A significant main effect of *sequence* may therefore be consistent with the effects of repetition suppression, whereby a reduction in neural response is observed upon repeated presentation of a stimulus (Desimone, 1996). This effect is believed to reflect the refined engagement of neural populations (Wiggs & Martin, 1998) and desensitisation through neuronal fatigue (Grill-Spector et al., 2006).

Self-generated stimuli were found to produce significantly smaller P2 amplitudes compared to those resulting from externally-generated events. Although the functional significance of the P2 remains relatively poorly understood, several lines of evidence have implicated the component in attentional processes. This includes the well-established ‘processing negativity’ effect (Hillyard et al., 1973), in which heightened attention to stimuli results in a negativity that spans the N1 and P2 range. Attention-related suppression of the P2 has also been observed independently of N1 effects, as an apparent result of task relevance (García-Larrea et al., 1992; Novak et al., 1992) and alertness (Colrain et al., 2000). In particular, it has been proposed that suppression of the P2 may reflect an executive control process supporting withdrawal of attention from non-relevant stimuli (García-Larrea et al., 1992). Reduced P2 amplitude for self-generated stimuli may therefore suggest that these were subject to heightened attentional control compared with levels allocated to stimuli produced by externally-generated events. This finding supports the notion that sensory attenuation may be partly attributable to effects involving attention, including its withdrawal from non-relevant stimuli as indexed by reduced P2 amplitude.

Interestingly, the suppressive effect of temporal predictability on N1 amplitude (i.e., *cued listening* versus *uncued listening)* was followed by relative negativity that was statistically significant at its peak approximately 200 ms post-stimulus (i.e., the N2b analysis window). This was not followed by an apparent P3 and was therefore unlikely to reflect influences associated with the N2b component, as the N2b requires attention to eliciting stimuli and is always accompanied by a P3 (Folstein & Van Petten, 2008; Pritchard et al., 1991). Instead, it may also be attributable to attentional modulation of the P2, which has been found to be larger and occur later in lower states of arousal, such as when transitioning from wakefulness to sleep (Colrain et al., 2000). Reduced P2 amplitudes in the temporally-predictable *cued listening* condition may therefore reflect greater preparedness for withdrawal of attention to cued stimuli. That this suppression occurred most prominently at frontal sites (see Fig. 4.3C) is also consistent with the effects of attention that have previously been observed with regard to the P2 component (García-Larrea et al., 1992; Novak et al., 1992).

Findings in relation to the N2b have particular relevance to understanding the role of action-effect prediction in motor control. A significant interaction was observed between *sequence* and *volition* (i.e., *uncued self-generation* in comparison with *cued self-generation* and both *listening* conditions), involving a prominent N2b in the *two-tone* variant of the *uncued self-generation* task that was not apparent in the *one-tone* variety (see Fig. 4.4). In contrast, N2b components were not evident in either variant of the *cued self-generation, cued listening* or *uncued listening* conditions. Research has implicated the N2b in error monitoring processes relating to self-generated sensations, with evidence to suggest that larger component amplitudes occur in response to unexpected task-relevant stimuli (Ferdinand et al., 2008; Ferdinand et al., 2015). This finding may therefore be consistent with the notion that volitional action involves comparison of the intended and actual outcomes to movement, while stimulus-driven action may be enacted with less regard for its specific sensory effects. In conjunction with recent evidence demonstrating differences in sensorimotor processing, this result highlights the need to distinguish between these forms of movement in research examining neurophysiological responsivity to self-generated stimuli.

Our results may also have relevance to understanding the mechanisms that give rise to one’s sense of agency. Because the selection of a motor action is based on an agent’s expectations regarding its capacity to achieve intended outcomes, sense of agency is believed to also relate to the alignment of predicted and actual sensory experience (see Haggard, 2017). Evidence for this relationship has been provided by research into the phenomenon of intentional binding, whereby the perceived interval between deliberate action and subsequent stimulus is reduced (Haggard et al., 2002). Moore and Haggard (2008) found that, for an action that does not consistently result in the presentation of a stimulus, temporal binding of the action (i.e., the degree to which it is experienced as having occurred later in time) is larger when stimuli are subsequently presented than when they are not. This suggests that intentional binding may retrospectively affect the perceived timing of action, based on resulting sensations. Significantly, for action not resulting in the presentation of a stimulus, Moore and Haggard (2008) found that intentional binding was larger when the prospective likelihood of action eliciting a stimulus was higher. Intentional binding thereby appears to be influenced by both prospective and retrospective factors, which contribute to one's sense of agency through the prediction of action-effects and their observation. Our findings suggest that, in contrast to volitional action, the processing of sounds resulting from stimulus-driven action is not influenced by predictions regarding its effects. For this reason, the retrospective aspect to one's assessment of agency may not be supported for this form of movement. Future research may seek to explore this possibility.

The study contained several limitations that warrant acknowledgment. Firstly, clear challenges are present with regard to disentangling effects relating to components with overlapping latencies. Future research may seek to distinguish effects involving the P2 and N2b in particular, given the close proximity of these components. Difficulty associated with the distinction of these components was most evident in the interpretation of effects associated with *temporal predictability*. Although the *cued listening* conditions were found to be more negative than the *uncued listening* conditions in the N2b analysis window (see Fig. 4.3C), this effect was attributed to differences in the P2 as this was supported by a stronger theoretical basis. This included the likelihood of differences in attentional control, and the absence of an apparent P3 in the *cued listening* condition. A second limitation relates to the presentation of trials for each condition type in separate blocks, which meant that overall levels of arousal may not necessarily be assumed to be equal. Although amplitudes of each analysed component may have been subject to arousal effects, a lack of consistency in the observed influence could serve to disconfirm this potential. For example, while the larger P2 component amplitudes for the *uncued listening* condition would indicate a general reduction in arousal, this is not consistent with larger N1 amplitudes observed for the same condition. Nevertheless, future research may seek to investigate the observed effects in a design that better controlled for potential differences in attention and arousal.

4.6 Conclusion

Findings from the present investigation highlight differences in the way that motor-based sensory prediction influences the processing of sound produced through volitional and stimulus-driven action. Self-generated tones with unpredictable sound frequencies were found to elicited N2b components when these were produced through volitional action, while self-generated tones with predictable sound frequencies did not. In contrast, N2b components did not appear in response to either predictable or unpredictable tone frequencies when these were produced by stimulus-driven action or externally-generated events. Given prior research implicating the N2b in error monitoring processes, this result appears to reflect differences in the way that unanticipated stimuli are treated when resulting from each form of action. Within the IFM framework, error signals may serve to support dynamic motor control (Miall & Wolpert, 1996) and inform one's perception of agency over sensations (Farrer & Frith, 2002). Our findings therefore reflect differences in the degree to which these functions are served for sensations resulting from each form of action.

Because the processing of sounds produced through stimulus-driven action did not exhibit effects relating to stimulus predictability, IFM-based suppression may be unable to account for the attenuation of sensations resulting from this form of action. Self-generated stimuli (i.e., those resulting from both stimulus-driven and volitional action) exhibited reduced P2 component amplitudes, compared with stimuli resulting from externally-generated events. Given that attentional control has previously been associated with reductions in P2 amplitude, this finding may therefore provide further support to the notion that sensory attenuation is associated attentional factors. Findings from the present study suggest that this may include differences in capacity for withdrawal of attention in particular.

Finally, the present study served to provide further caution against reliance on the N1 in examination of the sensory attenuation phenomenon. Significantly, N1 component amplitudes were not found to differ between self- and externally-generated sensations when these were made predictable in time. Although predictable tone frequencies were associated with a generalised reduction in N1 component amplitudes, evidence was identified to suggest that the effect of predictability did not differ between self- and externally-generated sensations. In each case, Bayesian analysis provided substantial evidence in favour of null hypotheses. While these findings may necessitate reconsideration of the manner in which sensory attenuation and other IFM mechanisms are studied, they also provide promising new avenues for investigation of sensorimotor effects involving the P2 and N2b.

5. Sensory processing of recurrent self-generated stimuli: Volition, gating and sensory attenuation

5.1 Abstract

Research has recently highlighted differences in the processing of self-generated stimuli based on the nature of the eliciting movement. This has included evidence that N1 amplitudes are larger for sounds resulting from volitional movement (i.e., occurring without external cues), compared with those resulting from action that is stimulus-driven (i.e., prompted by external stimuli). The present study aimed to compare sensorimotor processing of volitional and stimulus-driven movement, with particular focus on the effects of sensory gating and stimulus intervals. In particular, we examined the evoked potential of tones produced by sequences of each form of action. Median splits were conducted to separate trials, by condition and participant, on the basis of inter-trial interval. Through comparison with the evoked response of externally-generated tones, we also examined effects relating to the phenomenon of sensory attenuation (i.e., the reduced neurophysiological response to self- versus externally-generated stimuli). Participants (*N* = 38) were found to exhibited larger P50 amplitudes in response to tones that were produced by stimulus-driven action, reflecting lower levels of sensory gating. Larger N1 amplitudes were observed for self-generated tones that were separated by shorter inter-trial intervals, particularly those resulting from volitional movement, relative to externally-generated tones. In conjunction with documented effects relating to repetition suppression and prediction, we propose that these findings support the involvement of attentional mechanisms in volition-based enhancement of the auditory N1. This effect was such that the phenomenon of sensory attenuation may be reduced or, in some circumstances, reversed for stimuli produced through volitional movement.

5.2 Introduction

To effect change in its environment, an organism will initiate movement based on learned relationships between motor activity and sensation. For volitional movement (i.e., motor activity occurring in the absence of external cues), action-effect associations may be used to identify motor commands based on their capacity to achieve desired sensory outcomes (Wolpert et al., 1995). This mechanism is a central tenet to ideomotor theory, which proposes that intentional movement is selected and initiated on the basis of its predicted effects (see James, 1890; Shin et al., 2010). In contrast, stimulus-driven movement (i.e., motor activity that is prompted by an external cue) may involve predetermined responses to externally-generated events. This form of action has been described as a form of prepared reflex and is believed to be enacted with less regard for its sensory effects (see Hommel, 2000). Recent neurophysiological evidence has supported this notion, demonstrating processes of error monitoring in volitional movement that are absent with respect to stimulus-driven motor activity (Harrison, Christensen, et al., 2022). A distinction between volitional and stimulus-driven action is also supported by evidence reflecting computational differences in the use of learned motor-stimulus associations (Herwig et al., 2007) and distinct neuroanatomical pathways (see Fried et al., 2017; Fried et al., 2011; Haggard, 2008).

Differences have recently been observed in the primary cortical response to auditory stimuli produced by volitional and stimulus-driven movement. In two experiments by Harrison et al. (2021), the N1 component of the evoked response to self-generated tones was found to be larger when the eliciting action was uncued than when prompted by simple visual stimuli – an effect described henceforth as ‘volitional enhancement’. The auditory N1 is a large negative component that peaks 75 ms to 125 ms following sound onset and is believed to originate largely within the primary auditory cortex (see Zouridakis et al., 1998). It has been found to be sensitive to the intensity of stimuli, with louder sounds eliciting larger N1 amplitudes (Mulert et al., 2005). This finding may therefore suggest that stimuli produced through volitional action are perceived to be louder than those generated by stimulus-driven movement. As well as the intensity of a stimulus, N1 amplitude is believed to be influenced by one's capacity to predict its onset and characteristics (e.g., Lange, 2009; Weiskrantz et al., 1971). However, Harrison, Hughes, et al. (2022) excluded the potential role of predictability in volitional enhancement by demonstrating that the phenomenon is not sensitive to change in action-effect contingency (i.e., the likelihood of action eliciting a specific sound). Further research is therefore needed to elucidate the precise mechanisms and functional significance of volitional enhancement.

One avenue for exploration is the potential role of 'sensory gating'. This term has been used to describe an organism's capacity to suppress the neurophysiological response to extraneous or irrelevant sensory information (Venables, 1964). Electrophysiological research into sensory gating has traditionally focused on the P50, a positive component that occurs approximately 50 ms after sound onset (see Picton & Hillyard, 1974). When two identical sounds are presented in short succession, a reduction has been observed in the amplitude of P50 components elicited by the second stimulus (Fruhstorfer et al., 1970; Nagamoto et al., 1989). This effect has been attributed to change in pre-attentive arousal, reflecting a reduction in one's openness to integrating stimuli for sensory processing (Pratt et al., 2008). By influencing the intake of sensory material, such an effect may contribute to observed differences in the neurophysiological response.

While not specifically assessed, relative positivity was apparent in the results of the second experiment by Harrison et al. (2021) shortly after the onset of tones produced during sequences of stimulus-driven action. This feature of the evoked response had a latency and polarity that was consistent with the P50 component, and was absent for tones produced by volitional movement. The primary aim of this investigation was to therefore explore potential differences in sensory gating of sound resulting from volitional and stimulus-driven movement.

Effects associated with the interval between self-generated stimuli present another promising avenue for exploration. This is indicated by the findings of another recent study in which volitional enhancement was unexpectedly diminished (Harrison, Christensen, et al., 2022). The design of this investigation was highly similar to previous studies in which the phenomenon has been observed (Harrison, Hughes, et al., 2022; Harrison et al., 2021), aside from the introduction of prompts instructing participants to ‘slow down’ following sequential trials in which less than two seconds were left. This prompt introduced an effective floor to the spacing between trials, and resulted in longer inter-trial intervals (ITIs) compared to previous studies. For this reason, a secondary aim of the present investigation was to compare the effect of stimulus spacing on cortical response to sounds produced through volitional and stimulus-driven movement.

A final aim of the present investigation was to explore the influence of sensorimotor processes affecting each form of action on differences in the processing of self- and externally-generated stimuli. The term ‘sensory attenuation’ has been used to describe an observed reduction in the subjective intensity of self-generated stimuli, and corresponding neurophysiological response, compared with those produced externally (e.g., Blakemore et al., 1998; Schafer & Marcus, 1973). In the electrophysiological literature, this effect has typically been studied through examination of N1 amplitudes (Schröger et al., 2015). Sensory attenuation has previously been attributed to the operation of internal forward models (Miall & Wolpert, 1996), whereby motor-based predictions support suppression of the anticipated sensory outcomes to movement (Wolpert, 1997). Significantly, recent evidence has indicated that the primary cortical response to stimuli produced through volitional action does not differ from externally-generated stimuli when these are made predictable in time (Harrison et al., 2021). As a reduction in primary cortical response may only be observed for self-generated sounds resulting from stimulus-driven action (Harrison et al., 2021), sensorimotor differences may be informative to understanding the sensory attenuation phenomenon.

To examine effects associated with sensory gating and stimulus intervals, additional analyses were undertaken on data collected in the second experiment by Harrison et al. (2021). We compared P50 and N1 amplitudes of the evoked potential to tones that were externally-generated, and produced by volitional and stimulus-driven movement. Median splits were conducted to separate trials, by participant and condition, on the basis of inter-trial interval. Analyses of P50 component amplitudes were undertaken on an exploratory basis, without specific hypotheses. With regard to the N1, it was hypothesised that longer ITIs would be associated with a reduction in the volitional enhancement effect (i.e., a smaller difference between N1 amplitudes elicited by sound resulting from volitional and stimulus-driven movement).

5.3 Method

5.3.1 Participants

The final sample included 38 healthy participants (25 females), aged between 17 and 36 years (*M* = 21.38, *Mdn* = 19.22, *SD* = 4.80). Recruitment was undertaken through the University of New South Wales (UNSW) electronic participants recruitment system (SONA), following approval by the UNSW Human Research Ethics Advisory Panel (Psychology). Data from four additional participants were excluded due to self-reported diagnosis of a psychotic disorder (one participant) and recreational drug use within the preceding 48 hours (three participants).

5.3.2 Materials and design

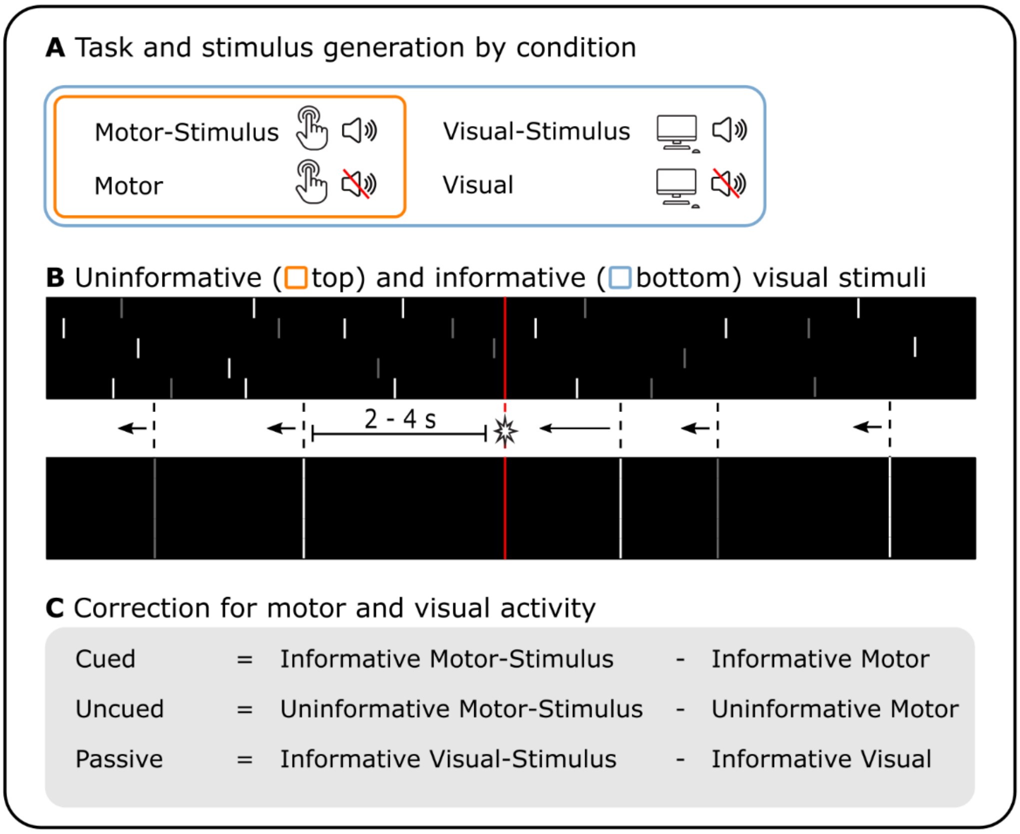
Participants were fitted with an EEG recording cap, containing a BioSemi ActiveTwo system with 64 Ag/Cl active electrodes positioned according to the extended 10:20 layout. Participants wore Sennheiser HD201 headphones and were seated facing a BenQ XL2420T computer monitor (24-inch, 1920 × 1080 resolution screen) at a distance of approximately 60 cm. Additional electrodes were placed below the left eye and adjacent to the outer canthus of each eye. They were also positioned on the tip of each participant’s nose, as well as left and right mastoids. Data acquisition was undertaken with a sampling rate of 2048 Hz, with grounding provided by the CMS and DRL cap electrodes.

Participants were instructed to place the index finger of their dominant hand on a keyboard button and to fix their gaze on a vertical red (fixation) line at the centre of the screen. The fixation line was one pixel wide and approximately six centimetres in length, corresponding to a visual angle of approximately 5.4°. In two *uninformative* block types (i.e., *motor-stimulus* and *motor* varieties), a sequence of randomly-spaced white line fragments appeared on the right of the monitor and moved leftward at a pace of approximately 3°/s. These line fragments were equal in length and distributed across five adjacent rows, collectively spanning the height of the fixation line (see Fig. 5.1). Participants were instructed to repeatedly press a keyboard button with an interval of approximately two to four seconds between each press. They were asked to vary the timing of their button presses so as to make the timing of each press unpredictable to an observer. In the *uninformative motor-stimulus* condition, each press elicited a 1000 Hz pure tone (85 dB, SPL/A-weighted, 10 ms ramp, 100 ms duration) via participant headphones. Silent audio tracks were triggered to mark each press in the *uninformative motor* condition. An AudioFile Stimulus Processor (Cambridge Research Systems) was used to support low-latency delivery of auditory stimuli in each condition, including both tones and silent audio tracks.

In four *informative* block types, vertical white (stimulus) lines that were equal in length to the fixation line appeared on the right of the screen and moved leftward at a constant rate of approximately 3°/s. Participants were instructed to press a keyboard button at the precise moment that each stimulus line reached the fixation line. In the *informative motor-stimulus* condition, a tone with the same parameters as described for the *uninformative motor-stimulus* condition was elicited by each button press, while each press resulted in the delivery of a silent audio track in the *informative motor* condition. Participants were instructed to passively watch the animation in *informative visual* and *informative visual-stimulus* conditions. In the *informative visual-stimulus* condition, a tone was delivered at the precise moment that each stimulus line intersected the fixation line. This tone had the same parameters as described for the *motor-stimulus* conditions above. A silent audio track was used to mark the passing of each stimulus line in the *informative visual* condition. The original experiment included variants of the *informative motor-stimulus* and *informative visual-stimulus* conditions that required participants to also keep a mental tally of the number of grey or white lines in each block and to report this afterwards (see Harrison et al., 2021). For simplicity, these counting variants have not been included in the present analyses. Descriptive statistics are included for these conditions in Appendix 4 (Table A4.1), demonstrating highly similar component amplitudes and other characteristics of the non-counting equivalents.

Trials were presented in blocks containing 30 trials of a single condition type. For each condition, three such blocks were presented across three sets (i.e., for a total of 90 trials per condition). The *uninformative motor-stimulus* condition was presented first in each set, followed by blocks of each other condition in randomised order.

Fig. 5.1. Protocol schematic and visual stimuli



A. A keyboard button was pressed to initiate events in the *motor-stimulus* and *motor* conditions, while these were computer-initiated in the *visual-stimulus* and *visual* conditions. Events involved presentation of 85 dB tones (1,000 Hz) in the *motor-stimulus* and *visual-stimulus* conditions. Silent audio tracks marked events in the *motor* and *visual* conditions. The orange and blue boxes indicate the stimulus generation conditions that were paired with *uninformative* and *informative* visual stimuli, respectively. **B.** In *uninformative* conditions, line fragments were randomly distributed across five adjacent rows and moved from right to left at a constant rate that corresponded to five fragments (i.e., one per row) every three seconds. Participants were instructed to press a keyboard button, at will, every two to four seconds approximately. In the *informative motor-stimulus* and *informative motor* conditions, participants were instructed to press the keyboard button at the precise moment that each passing line intersected with the red fixation line. Participants passively observed as computer-initiated tones were presented at these moments during the *informative visual-stimulus* condition. C. Three analysis conditions were produced based on the six experimental conditions, representing motor-corrected *uncued* and *cued* conditions, as well as a visual-corrected *passive* condition. Note that these were subsequently disaggregated into *short* and *long* ITI conditions, based on a median split of trials by ITI length for each participant. As a result, six conditions were included in analyses, representing *short* and *long* ITI variants of the three analysis conditions (i.e., *cued*, *uncued* and *passive*).

5.3.3 EEG Processing

BrainVision Analyser (Version 2.2.0; Brain Products GmbH, Gilching, Germany) was used to process EGG data offline. All cap electrodes were referenced to the nose electrode. A notch filter (50 Hz) was applied, as well as a phase-shift free half-amplitude Butterworth band-pass filter (0.1 Hz to 30 Hz) with 12 dB/Oct slope. Trials were then segmented into 600 ms epochs, starting 200 ms prior to each event. A vertical electro-oculogram (EOG) was developed based on recordings from the electrode below each participant's left eye in conjunction with Fp1. A horizontal EOG was produced using recordings from the electrodes placed adjacent to the outer canthus of each eye. Eye movement artefacts were corrected using the approach described by Miller et al. (1988), based on the method by Gratton et al. (1983). Epochs were excluded if, following eye movement correction, they were found contain peak-to-peak amplitudes in excess of 200 µV. Baseline correction was then applied using average voltage recordings in the 200 ms prior to each event.

To isolate activity associated with auditory stimuli, ERPs for the *motor-stimulus* and *visual-stimulus* conditions were corrected by subtracting those of the *motor* and *visual* conditions respectively. Six experimental conditions thereby supported calculation of three conditions, which we describe as *cued*, *uncued* and *passive* (see Fig. 5.1C). Median splits were conducted to separate trials, by condition and participant, on the basis of ITI. The first trial of each block, as well as those with an ITI above 5 s were excluded prior to calculation of median values. The median split provided two grand-averaged waveforms for each condition, representing trials that involved *shorter* and *longer* ITI.

Component peaks were found using the collapsed localiser method (see Luck & Gaspelin, 2017), with mean amplitudes then calculated for each participant based on 20 ms windows centred around these peaks. The collapsed localiser method involves identifying a single latency for each component based on average waveforms across all participants and conditions in which the component is believed to be present. In accordance with prior investigations (see Bramon et al., 2004), P50 analyses were based on recordings at the Cz electrode site. The P50 was identified as the most positive local maximum between 0 ms and 50 ms in a waveform containing average recordings from *cued* conditions. Using this method, the peak amplitude of the P50 was found to have occurred 39 ms post-stimulus. Analyses of the P50 amplitude were therefore based on average recordings between 29 ms and 49 ms post-stimulus. In accordance with previous research, N1 amplitudes were analysed using pooled recordings at Fz, FCz and Cz (Harrison et al., 2021; Whitford et al., 2017). The N1 peak was identified as the most negative local minimum between 25 ms and 175 ms in a waveform containing average recordings from the six conditions (i.e., *short* and *long* variants of the *cued*, *uncued* and *passive* conditions). This was found to have occurred 92 ms post-stimulus, with analyses of N1 amplitudes therefore based on average recordings between 82 ms and 102 ms post-stimulus.

5.3.4 Statistical Analyses

Two 2 x 3 repeated measures ANOVAs were conducted to assess the main effects of *ITI* (i.e., *short* versus *long*, based on a median split for each participant) and *task* (i.e., *cued*, *uncued* and *passive*), as well as their interaction, on P50 and N1 component amplitudes respectively. Planned comparisons involved two orthogonal contrasts of *task* (i.e., *cued*, *uncued* and *passive*), supporting investigation of the effects of *self-generation* ([1, 1, -2]) and *volition* ([-1, 1, 0]). These contrasts were not corrected for multiple comparisons, given that they were orthogonal and selected a priori.

To assess consistency in ITI between conditions, an additional 2 x 3 repeated measures ANOVA was conducted. This examined potential differences in ITI across experimental conditions, including with respect to the presence of *auditory stimuli* (i.e, *motor-stimulus/visual-stimulus* versus *motor/visual*) and *task* (i.e., *cued*, *uncued* and *passive*).

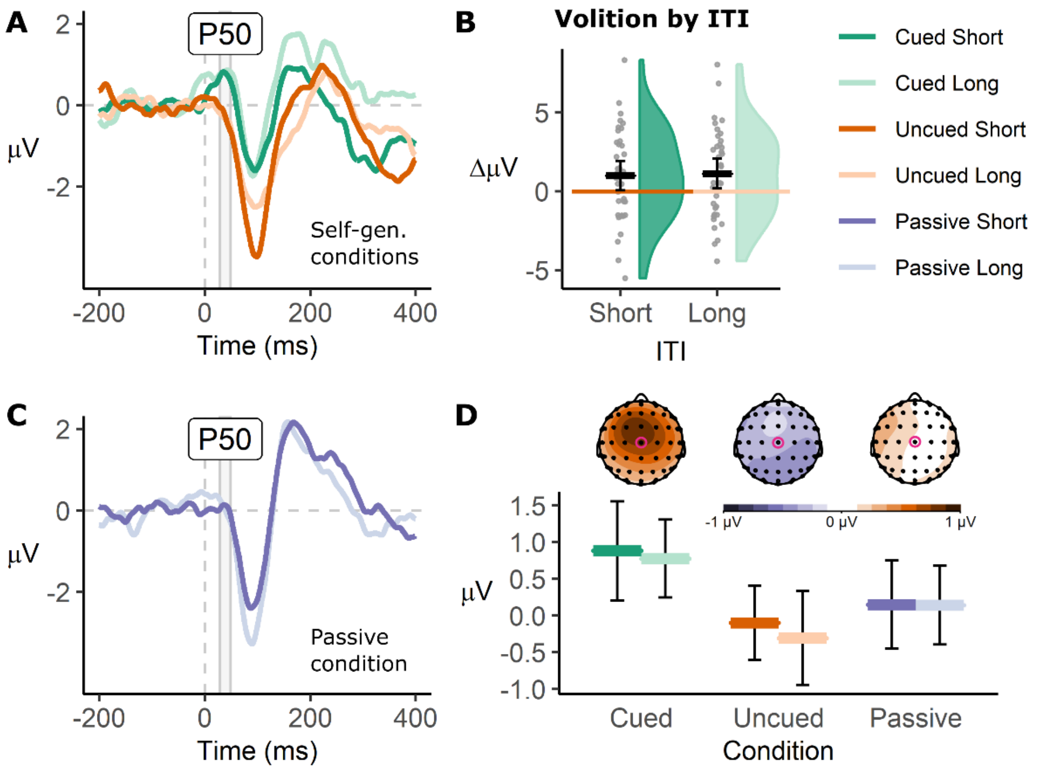
5.4 Results

5.4.1 P50

A 2 x 3 repeated measures ANOVA was conducted to assess the main effects of *ITI* and *task*, as well as their interaction, on P50 amplitudes. Two orthogonal contrasts supported examination of the effects of *self-generation* and *volition* (see Statistical Analyses). The Greenhouse-Geisser method (Geisser & Greenhouse, 1958) was used to correct for non-sphericity identified by Mauchly’s test (Mauchly, 1940). The ANOVA revealed a significant main effect of *task*, $F(1.91, 70.85) = 5.97$, $p = .004$, $\eta_p^2 = 0.14$. Planned comparisons indicated that the effect of *volition*, contrasting tasks that involved self-generated stimuli (i.e., *uncued* versus *cued*), was statistically significant, $t(74) = -2.31$, $p = .023$, $d = -0.44$ (see Fig. 5.2B). The effect of *self-generation* (i.e., comparing the *passive* task with those that involved self-generated stimuli) was not found to be statistically significant, $t(74) = 0.66$, $p = .508$, $d =$

0.15. Neither the main effect of *ITI*, nor interactions between *ITI* and either *self-generation* or *volition*, were statistically significant either. Results of the ANOVAs and planned comparisons are reported in full in Appendix 4 (Tables A4.5 and A4.6, respectively).

Fig. 5.2. P50 Analyses

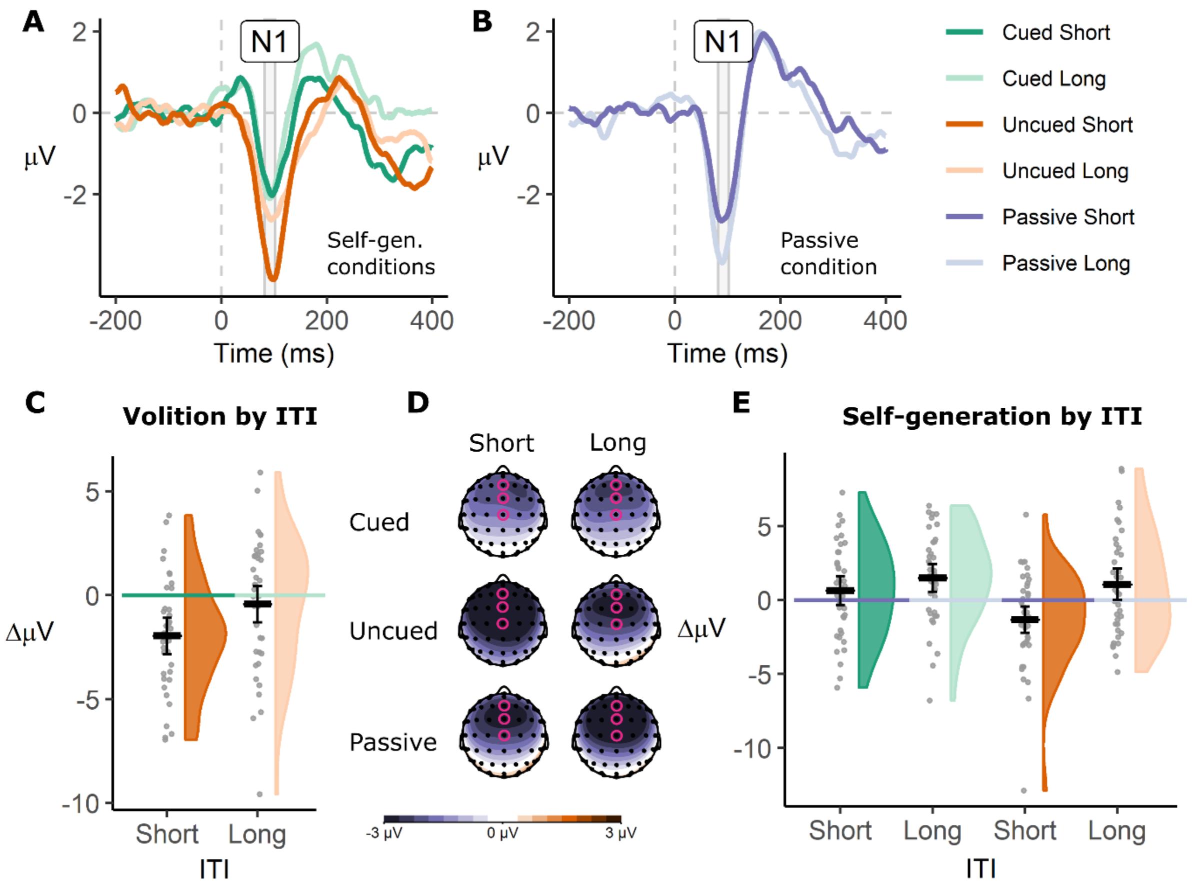


A. Grand-average recordings at Cz, demonstrating mean amplitude by *ITI* (i.e., *short* and *long*) for *self-generation* tasks (i.e., *cued* and *uncued*). **B.** Within-subject differences in mean P50 amplitude between *cued* and *uncued* task by *ITI*, demonstrating the effect of *volition*. **C.** Grand-average recordings at Cz, demonstrating mean amplitude by *ITI* (i.e., *short* and *long*) for the *passive* task. **D.** Mean voltages and 95% CIs for P50 amplitudes by *task*, as well as corresponding topographic voltage maps.

5.4.2 N1

A second 2 x 3 repeated measures ANOVA was conducted to assess the main effects of *ITI* and *task*, as well as their interaction, on N1 amplitudes. Planned comparisons again involved orthogonal contrasts of *task* (i.e., *cued*, *uncued* and *passive*), supporting investigation of *self-generation* ([1, 1, -2]) and *volition* ([-1, 1, 0]). As Mauchly's test (Mauchly, 1940) again indicated non-sphericity, which was corrected using the Greenhouse-Geisser method (Geisser & Greenhouse, 1958). The ANOVA revealed a significant main effect of *task*, $F(1.95, 72.18) = 5.87$, $p = .004$, $\eta_p^2 = 0.14$. Planned comparisons revealed a statistically significant effect of *volition*, $t(74) = -3.80$, $p < .001$, $d = -0.72$, reflecting the difference between *cued* and *uncued* tasks. In contrast, the effect of self-generation was not found to be statistically significant, $t(74) = -0.78$, $p = .440$, $d = -0.18$. While the effect of *ITI* was not found to be statistically significant overall, $F(0.95, 35.14) = 0.27$, $p = .605$, $\eta_p^2 = 0.01$, a significant interaction was observed between *task* and *ITI*, $F(1.90, 70.29) = 6.07$, $p = .004$, $\eta_p^2 = 0.14$. Planned comparisons identified significant interactions between *ITI* and both *volition*, $t(111) = 2.21$, $p = .029$, $d = 0.51$, and *self-generation*, $t(111) = 2.71$, $p = .008$, $d = 0.52$ (see Fig. 5.3C and Fig. 5.3E).

Fig. 5.3. N1 Analyses



A-B. Pooled grand-average recordings at Fz, FCz and Cz, demonstrating mean amplitude by ITI (i.e., *short* and *long*) for (A) self-generation tasks (i.e., *cued* and *uncued*) and (B) the *passive* task. **C.** Within-subject differences in mean N1 amplitude between *cued* and *uncued* tasks by *ITI*, demonstrating the interaction between *volition* and *ITI*. **D.** Topographic voltage maps, demonstrating N1 distribution by *task* (i.e., *cued*, *uncued* and *passive*) and *ITI* (i.e., *short* and *long*). **E.** Within-subject differences in mean N1 amplitude between the *passive* and *self-generation* tasks by *ITI*, demonstrating the interaction between *self-generation* and *ITI*.

5.4.3 Behavioural

A 2 x 3 repeated measures ANOVA was conducted to assess consistency in mean ITI across experimental conditions. In particular, this examined potential differences based on the presence of *auditory stimuli* (i.e., *motor-stimulus/visual-stimulus* versus *motor/visual*) and analysis *task* (i.e., comparing *cued*, *uncued* and *passive*). Mauchly's test (Mauchly, 1940) indicated non-sphericity, which was corrected using the Greenhouse-Geisser method (Geisser & Greenhouse, 1958). Results from the ANOVA did not reveal a statistically significant relationship between mean ITI and the presentation of *auditory stimuli*, $F(0.51, 19.02) = 1.98$, $p = .168$, $\eta_p^2 = 0.05$, the *task*, $F(1.01, 37.49) = 1.37$, $p = .262$, $\eta_p^2 = 0.04$, or their interaction, $F(1.01, 37.49) = 2.03$, $p = . 138$, $\eta_p^2 = 0.05$ (see Table A4.3 for detail).

5.4.4 Power Analyses

Post hoc power analyses explored the power (1 - β) of the sample ($N = 38$) to assess small, medium and large effect sizes, according to standardised reporting conventions (Cohen, 1988). The sample was found to be sufficient to detect small ($\eta_p^2 = .01$), medium ($\eta_p^2 = .06$) and large ($\eta_p^2 = .14$) two-level repeated measures main effects with powers of .227, .858, and .998, respectively. With respect to three-level repeated measures main effects, the sample was found to achieve powers of .246, .927, and < .999 respectively.

5.5 Discussion

The primary aim of this investigation was to explore potential differences in sensory gating of sound produced through volitional and stimulus-driven movement. This was achieved through comparison of the auditory evoked response to tones resulting from sequences of each form of action. Findings indicated larger P50 amplitudes in response to tones produced by stimulus-driven movement, compared with those generated through volitional action (i.e., *cued* versus *uncued* conditions). This suggests that stimuli resulting from volitional movement may be subject to pre-attentive sensory gating in a manner not applied to those produced through stimulus-driven action.

A secondary aim of the study was to compare effects involving the interval between stimuli on cortical responses to sound produced through volitional and stimulus-driven movement. To support this analysis, median splits were conducted to separate trials, by condition and participant, on the basis of ITI. Consistent with our hypothesis, a shorter ITIs were found to be associated with more negative N1 components when resulting from stimuli produced through volitional action, compared with those generated by stimulus-driven movement. This finding may therefore account for the diminishment of volitional enhancement in experiments that have implemented a lower bound to the interval between trials (Harrison, Christensen, et al., 2022).

Interestingly, our findings suggest that stimuli produced through volitional action are subject to more sensory gating despite being associated with a larger primary cortical response (i.e., as reflected by reduced P50 and increased N1 amplitudes). One potential explanation for this apparent contradiction is that sensory gating may be increased for stimuli resulting from repeated volitional action *in response to* higher levels of activity in the primary auditory cortex (i.e., suppressing new sensory information when the level of cortical activation is already high). This notion is consistent with results demonstrating that the difference in P50 amplitude between volitional and stimulus-driven movement was not sensitive to ITI, despite an apparent absence of P50 components from studies with longer inter-trial intervals (Harrison, Hughes, et al., 2022; Harrison et al., 2021). These results may therefore suggest that the difference in P50 amplitude develops over repeated trials, in contrast to volitional enhancement of N1 amplitude following the production of two self-generated stimuli in short succession. In this manner, heightened cortical activation with repeated stimuli may be counterbalanced by progressive growth in sensory gating. A second possibility is that other mechanisms influencing primary cortical response are sufficient to counteract the effects of sensory gating. This may include the influence of attentional factors, which previous research has indicated may contribute to the volitional enhancement effect (Harrison, Hughes, et al., 2022). In other words, despite a reduction in the intake of sensory information, heightened attention to stimuli resulting from volitional action may contribute to higher levels of cortical activation.

Differences in the allocation of attention and sensory gating of stimuli produced through each form of action may hold particular relevance to understanding conscious agency in the production of sensation. While an organism is free to determine the nature and timing of volitional action, aspects of control are relinquished to an external cue during stimulus-driven movement. For this reason, distinctive mechanisms of volitional and stimulus-driven action have been the focus of research seeking to understand perceptions of conscious agency in movement (see Haggard, 2008). Neurophysiological phenomena involving the supplementary motor area (SMA) and pre-SMA have been particularly informative, given evidence that these regions contribute more to volitional movement than stimulus-driven action (Debaere et al., 2003; Fried et al., 2011). Interestingly, stimulation of these regions has been shown to result in an “urge to move” specific body parts (Desmurget et al., 2009; Fried et al., 1991). While higher levels of stimulation to either the SMA or primary motor cortex elicit actual movement, the latter is not accompanied by a sense of deliberate intent (Fried et al., 2017; Fried et al., 1991; Haggard, 2011). To the degree that intentional movement requires allocation of attentional resources, modulation of the cortical response to stimuli produced through volitional action may depend on pre-attentive sensory gating as opposed to suppressive attentional effects. Our results may therefore support a framework in which stimuli resulting from volitional action are attended as part of one’s conscious experience of movement, while the overall level of stimulation is regulated by sensory gating mechanisms. In contrast, the neurophysiological response to tones resulting from stimulus-driven action may be suppressed through selective attentional processes.

A final aim of the study was to explore the relationship between sensorimotor processes affecting each form of action and differences in the processing of self- and externally-generated stimuli. A significant interaction between *ITI* and *self-generation* (i.e., contrasting *passive* with both *cued* and *uncued*) suggested that the interval between trials differentially affected N1 amplitudes resulting from self- and externally-generated stimuli. Specifically, shorter ITIs were associated with larger (i.e., more negative) N1 components when resulting from self-generated stimuli compared with those of externally-generated stimuli. This finding may support the notion that volitional enhancement reflects the degree to which one experiences a sense of agency over self-generated stimuli. It has been suggested that voluntary action lies at one end of a continuum that has simple reflexes at the other (Haggard, 2008). While less control may be exerted over motor activity when enacted in response to visual cues, a greater sense of agency may be expected compared with that experienced in relation to passively observed stimuli. Taken together, the present findings may suggest that sensory attenuation (i.e., the reduced neurophysiological response to self-generated stimuli compared with those produced externally) is reduced when the interval between stimuli is shortened. For volitional movement, a reduction in the interval between stimuli may even contribute to a reversal of the phenomenon.

In conjunction with the documented effects of repetition suppression and non-motor identity prediction, our findings may implicate attentional mechanisms in the volitional enhancement effect. Repetition suppression describes an observed reduction in the neural response elicited by repeated stimuli (see Desimone, 1996), and is among the most widely studied neurological phenomena (Auksztulewicz & Friston, 2016). While previous theories held that repetition suppression emerges as a result of neuronal fatigue (Grill-Spector et al., 2006) or refined engagement of neuronal populations (Wiggs & Martin, 1998), more recent evidence supports the role of heightened predictability over successive exposures

(Auksztulewicz & Friston, 2016; Mayrhauser et al., 2014; Summerfield et al., 2008). Like volitional enhancement, repetition suppression is influenced by the interval between stimulus presentations, with a larger reduction in neuronal response observed for stimuli presented in close succession (Brozinsky et al., 2005). Significantly, attention has been found to reverse the effect of prediction-based suppression of neuronal activity (Kok et al., 2012). Heightened attention to stimuli resulting from volitional movement, compared with those resulting from either stimulus-driven action or externally-generated events, may therefore be consistent with the observed effects. In this manner, volitional enhancement may represent a reversal of repetition suppression based on heightened attention to the outcomes of voluntary movement.

There were several limitations to the present study that warrant acknowledgement. Firstly, our investigation has relied on data collected in the course of another investigation (Harrison et al., 2021). As these have been disaggregated in the current study (i.e., involving a median split by ITI), the reduced number of trials per condition has constrained signal-to-noise ratios. Despite this, robust statistical effects and an absence of outliers (e.g., as demonstrated in within-subject differences depicted in Fig. 5.2 and Fig. 5.3) serve to validate conclusions. Nevertheless, future research may seek to explore these effects with a larger sample or more trials per condition. A second limitation to the present investigation relates to the extrapolation of neurophysiological effects to conclusions regarding subjective experience. In particular, our discussion has assumed that stimuli resulting from movement undertaken in the absence of external cues may be associated with a greater sense of agency than those produced in response to visual prompts. This distinction is in accordance with previous research, which has emphasised computational differences in the use of learned motor-stimulus associations (Herwig et al., 2007) and distinct neuroanatomical pathways (see Fried et al., 2017; Fried et al., 2011; Haggard, 2008). However, the relationship between neurophysiological phenomena distinguishing these forms of action and differences with respect to the subjective experience of resulting sensations remains to be investigated. For example, future research may seek to directly examine the relationship between the phenomenon of volitional enhancement and reported perceptions of agency in the production of sensations.

5.6 Conclusion

In conclusion, the present investigation has highlighted differences in sensory gating of stimuli produced through volitional and stimulus-driven movement. Larger P50 amplitudes were observed for sounds produced through motor activity when cued using simple visual stimuli, compared with those resulting from uncued movement. As suppression of the P50 has previously been taken to reflect pre-attentive inhibition of one's neurophysiological response (see Desimone, 1996), this finding reflects a relative reduction in such gating for stimuli that result from stimulus-driven movement. Our findings also revealed a significant interaction between stimulus intervals and the amplitude of N1 components elicited by each form of action. Larger (i.e., more negative) N1 amplitudes were observed following shorter inter-trial intervals when stimuli were produced through volitional movement, compared with those resulting from stimulus-driven motor activity. This finding may account for the diminishment of volitional enhancement in studies that have required longer intervals between participants' generation of stimuli (Harrison, Christensen, et al., 2022). As a corollary to this effect, we have discussed evidence to suggest that the phenomenon of sensory attenuation may be reduced and potentially reversed for stimuli resulting from volitional action when the interval between trials is reduced (i.e., stimuli produced in such a manner may be associated with larger N1 amplitudes than identical stimuli when externally-generated). In conjunction with documented effects relating to repetition suppression and prediction, we proposed that these findings support involvement of attentional mechanisms in the volitional enhancement phenomenon.

6. General discussion

The overall aim of this body of work was to investigate processes involved in the IFM, including factors affecting the production and processing of self-generated stimuli compared with those produced externally. In four separate investigations, potential confounds to research into sensory attenuation were explored, as well as effects involving volition, attention, action-effect prediction, error monitoring and sensory gating. The carefully controlled paradigms we developed were also used to facilitate comparison of ERP components reflecting motor preparation for volitional (i.e., uncued) and stimulus-driven (i.e., cued) movement, as well as the processing of resultant stimuli. Together, the findings of these investigations provide new insight into the mechanisms underlying sensory attenuation and highlight the importance of distinguishing processes associated with volitional and stimulus-driven movement. A summary and synthesis of key findings is provided below, followed by discussion of these results in the context of the wider literature and future research directions.

6.1 Summary of key findings

6.1.1 Study 1

In the first investigation, we sought to examine the influence of temporal predictability and temporal control on the phenomenon of sensory attenuation (i.e., the reduced subjective intensity and neurophysiological response to self-generated stimuli compared with those produced externally). This was achieved by comparing the amplitudes of auditory N1 components in four conditions that differed with respect to these factors. An *uncued self-generation* condition involved production of sound stimuli by button-presses that were made according to participants' own timing (i.e., self-paced). In a *cued self-generation* condition, these same sounds were produced through button-presses that were cued by visual stimuli in a ‘ticker-tape’ style display. After correction for visual and motor activity (i.e., through subtraction of waveforms generated by actions that did not elicit sound stimuli but were otherwise identical), differences in the ERPs elicited in these conditions were taken to reflect the effects of temporal control. An *uncued listening* condition involved passive observation of sound stimuli that were unpredictable in time, while the *cued listening* condition involved stimuli that were made temporally predictable by the same ‘ticker-tape’ presentation that was used to cue action. After correction for visual-evoked activity (i.e., through subtraction of waveforms generated in the absence of sound stimuli but otherwise identical circumstances), differences in the ERPs elicited in the conditions were taken to reflect effects associated with temporal predictability.

Examination of auditory N1 amplitudes revealed significant effects involving both temporal predictability and temporal control. A reduction in the amplitude of N1 components elicited in the *cued listening* condition, compared with those in the *uncued listening* condition, reflected a reduced cortical response associated with increased temporal predictability. In contrast, temporal control was found to result in enhanced N1 amplitudes (i.e., larger N1 components were observed in the *uncued self-generation* condition compared with those in the *cued self-generation* condition). Comparison of *cued self-generation* and *cued listening* indicated that sensory attenuation of the N1 prevails when controlling for both the suppressive effect of temporal predictability and enhancement resulting from temporal control. These results were replicated in a second experiment, which included conditions that also required participants to keep tally of the number of white or grey lines on the ‘ticker-tape’ presentation. While manipulation of visual attention was evidenced by increased N2b amplitudes in these conditions, this was not found to affect N1 component amplitudes suggesting that the observed sensory attenuation was not sensitive to such effects. Overall, these findings highlight the importance of controlling for both temporal predictability and temporal control in studies examining the phenomenon of sensory attenuation.

6.1.2 Study 2

Our second investigation sought to explore the influence of action-effect contingency on processes involved in volitional (i.e., uncued) and stimulus-driven (i.e., cued) movement, including with regard to both motor preparation and processing of resultant stimuli. The primary motivation for this experiment was to explore the potential influence of action-effect contingency on the enhanced cortical response (i.e., N1 amplitude) found to be associated with temporal control in the first study. A secondary aim was to investigate proposed differences in the use of action-effect prediction to initiate volitional and stimulus-driven movement.

We implemented a similar paradigm as described for the first investigation. In this study, participants were instructed to respond to a small arrow at the point of fixation by pressing a button with the index finger on the hand to which this pointed. While one hand elicited a tone each time the button was pressed (i.e., *100% motor-stimulus* condition), the other elicited a tone 50% of the time (i.e., *50% motor-stimulus* condition) and a silent audio track on other trials (i.e., *50% motor* condition). As trials were randomised within blocks, action-effects were unpredictable in the 50% condition. In *volitional* conditions, participant action was self-paced (i.e., uncued). The ‘ticker-tape’ stimuli were again used to cue action in the *stimulus-driven* conditions. Motor activity was corrected using the same method as described for the first study, based on equivalent conditions that did not present sound stimuli but were otherwise identical (i.e., *0% motor* condition).

Our findings with respect to the N1 replicated those of the first investigation by demonstrating reduced amplitude in response to tones elicited by *stimulus-driven* action compared to those resulting from *volitional* movement. Contrary to hypotheses, action-effect contingency was not found to influence this relationship and Bayesian analyses provided substantial evidence in favour of a null effect. Similarly, while action-effect prediction was found to influence the amplitude of RP components (i.e., larger amplitude preceding action with 100% likelihood of eliciting a tone, compared to those with 50% likelihood), the magnitude of this effect was not found to differ between *volitional* and *stimulus-driven* movement. Findings of an exploratory analysis revealed lateralised activity at the time of enactment and shortly following (i.e., the LEP and LPP), which was larger for *stimulus-driven* movement than *volitional* action. Based on experimental factors and shared characteristics with more established components, we proposed that these effects may reflect the termination of attention used in the production of movement and suppression of attentional capture by resultant stimuli. Taken together, we propose that these findings contribute to a growing body of evidence supporting attribution of the sensory attenuation phenomenon to attentional mechanisms rather than prediction-based internal forward models.

6.1.3 Study 3

In a third investigation, we aimed to compare the influence of stimulus predictability on the neurophysiological response to self- and externally-generated stimuli. Given findings from the previous studies, we sought also to differentiate sensorimotor processes in stimulus-driven and volitional action, and to assess and control for the effect of temporal predictability. A similar paradigm was used to that of the first investigation in particular, including replication of the *uncued self-generation, cued self-generation, uncued listening* and *cued listening* conditions. In this experiment, sound stimuli consisted of sequences containing the same tone frequency, or two different tone frequencies that were randomly intermixed and therefore unpredictable. These *one-tone* and *two-tone* conditions were presented in separate blocks. To reduce potential effects associated with repetition suppression, a simple prompt was present to participants to request that they ‘slow down’ following button-presses that were made within 2000 ms of the preceding trial. As with other studies, each condition was corrected for visual and motor activity through subtraction of waveforms produced in tasks that were without sound stimuli but otherwise identical. In addition to the auditory N1, analyses were conducted on the P2 and N2b components to support examination of potential differences in attentional control and error monitoring respectively.

Analyses of the N2b component revealed a significant interaction between volition (i.e., contrasting *uncued self-generation* with other conditions) and sequence (i.e., *one-tone* and *two-tone*). In particular, prominent N2b components were elicited by stimuli in the *two-tone* variant of the *uncued self-generation* condition that were absent in other conditions (i.e., including *cued self-generation*). It was proposed that this finding may reflect higher levels of error monitoring during *volitional* action compared with *stimulus-driven* movement. Compared with externally-generated stimuli, self-generated tones exhibited reduced P2 component amplitudes. Evidence was also explored with respect to reduced P2 component amplitudes in the *cued listening* condition compared with those in the *uncued listening* condition. These findings may indicate increased attentional control over stimuli resulting from one’s own actions, and externally-generated stimuli when these are able to be predicted in time. Interestingly, this investigation did not replicate previous findings with respect to the effect of temporal control on N1 amplitudes. Although the reasons for this were not immediately apparent, it was noted that the experiment involved longer average intervals between trials due to the introduction of a prompt asking participants to ‘slow down’ following self-paced button presses made in short succession.

6.1.4 Study 4

The fourth investigation aimed to explore sensorimotor processes involved in volitional and stimulus-driven movement, with particular focus on the effects of sensory gating and stimulus intervals. The potential contribution of these factors was also explored with respect to their influence on sensory attenuation. The effects of sensory gating have typically been studied in paired-click paradigms, involving examination of the evoked response to two identical sounds presented in short succession (Fruhstorfer et al., 1970). These have revealed a reduction in the P50 amplitude elicited by the second stimulus (e.g., Fruhstorfer et al., 1970; Nagamoto et al., 1989), which is believed to reflect pre-attentive suppression of extraneous or irrelevant sensory information (Pratt et al., 2008). As our investigations utilised an experimental design involving repetitive presentation of sound stimuli (i.e., sequences of self- and externally-generated tones), we considered the potential effects of sensory gating relevant to understanding differences in evoked activity. The potential effect of inter-stimulus intervals (ITIs) was also considered due to the fact that differences in the N1 amplitude elicited by stimuli resulting from volitional and stimulus-driven action were unexpectedly diminished in the third study. As ITIs were longer in this investigation due the introduction of a prompt asking participants to ‘slow down’ following trials produced in short succession, we anticipated that increased intervals between stimuli may have contributed to this finding.

To examine effects associated with sensory gating and stimulus intervals, additional analyses were undertaken on data collected in the second experiment of Study 1. Median splits were conducted to separate trials, by participant and condition, on the basis of ITI. We then compared P50 and N1 amplitudes of the evoked potential to tones that were externally-generated, and produced by volitional and stimulus-driven movement. The results of our analyses indicated that tones produced by stimulus-driven action elicited larger P50 amplitudes than those produced by volitional movement or externally-generated events, reflecting lower levels of sensory gating. With regard to stimulus intervals, shorter ITIs were associated with larger N1 amplitudes when elicited by self-generated tones, particularly when resulting from volitional movement, compared with those produced by externally-generated events. This effect was such that the phenomenon of sensory attenuation was reversed for stimuli produced by volitional action in short succession.

6.2 Implications for sensory attenuation

The overarching aim of this body of work was to investigate factors influencing the phenomenon of sensory attenuation. This effect was operationalised as a reduction in the auditory N1 amplitudes to self-generated stimuli compared with those produced externally, in a manner that was consistent with previous EEG/MEG investigations of sensory attenuation (e.g., Baess et al., 2011; Bäß et al., 2008; Bednark et al., 2015; Cao et al., 2017; Curio et al., 2000; Ford, Gray, et al., 2007; Ford, Mathalon, Kalba, et al., 2001; Ford et al., 2014; Harrison et al., 2021; Heinks-Maldonado et al., 2005; Houde et al., 2002; Hughes et al., 2013a; Lange, 2011; Martikainen et al., 2005; Mifsud et al., 2016; Sanmiguel et al., 2013; Timm et al., 2013; Timm et al., 2016; Whitford et al., 2011). In addition to examining the potential influence of methodological confounds, we explored differences in sensory processing with relevance to proposed mechanisms of the IFM framework. In the following section, I discuss key findings with respect to effects involving temporal predictability, temporal control, action-effect prediction, and attention. Together, these results highlight important considerations with respect to the methodologies used to study sensory attenuation and the theoretical basis for its effects.

6.2.1 Temporal predictability

When stimuli are produced immediately in response to motor activity, the timing of these are inherently predictable to the individual responsible for their production. This is in contrast with externally-generated stimuli, which may or may not be predictable in time depending on the availability of sensory cues indicating their onset. Previous literature has demonstrated that increasing the temporal predictability of externally-generated stimuli, through rhythmic patterns (Lange, 2009) or visual cues (Schwartze et al., 2011; Sowman et al., 2012; Vroomen & Stekelenburg, 2010), results in a reduction in the neurophysiological response (i.e., N1 amplitude). This has been identified as a significant challenge to research exploring sensory attenuation, as much of the literature has not adequately controlled for inherent differences in the temporal predictability of self- and externally-generated stimuli.

Studies 1 and 3 assessed the influence of temporal predictability by comparing the evoked responses to uncued externally-generated sound stimuli (i.e., *uncued listening*) with those of externally-generated sound stimuli that were cued using basic visual stimuli (i.e., *cued listening*). In accordance with previous findings (Lange, 2009; Schafer & Marcus, 1973; Schwartze et al., 2011; Sowman et al., 2012; Vroomen & Stekelenburg, 2010; Weiskrantz et al., 1971), both studies revealed a significant reduction in auditory N1 amplitude for sounds that were made temporally predictable. As the auditory N1 reflects activation within the primary auditory cortex and has typically been the focus of sensory attenuation research, these findings highlight the importance of controlling for differences in temporal predictability when examining the phenomenon.

Interestingly, the results of Study 3 may suggest that temporal predictability is also associated with a reduction in the amplitude of P2 components (i.e., smaller amplitude in the *cued listening* condition, compared with *uncued listening*). Although this effect was observed in the N2b analysis window, we identified several reasons why we believe it is likely to reflect differences in the amplitude of the P2 component. Firstly, relative negativity in the *cued listening* condition was not accompanied by an apparent P3 component, which is known to co-occur with the N2b (Folstein & Van Petten, 2008; Pritchard et al., 1991). Secondly, previous evidence has also indicated that the P2 has a larger amplitude and occurs later in lower states of arousal (Colrain et al., 2000). We proposed that greater preparedness for withdrawal of attention to stimuli in the *cued listening* condition may have therefore contributed to smaller P2 components compared with those in the *uncued listening* condition. This was supported by the topography of the difference wave as well, which reflected suppression most prominently at frontal sites in a manner consistent with attentional effects on the P2 (García-Larrea et al., 1992; Novak et al., 1992).

While suppression of temporally-predictable stimuli was broadly consistent with theories proposing reduced cortical activation by predictable events (e.g., Friston, 2005, 2010), our results do not support the notion that these effects are associated with the prediction of stimulus properties *per se.* In particular, Study 3 examined potential interactions between the predictability of tone frequencies and timing. The results of Bayesian analyses reflected substantial evidence against the presence of an interaction between these variables, including with respect to the amplitudes of both the N1 and P2 component. That is, prediction of the identity of a stimulus (i.e., tone frequency in this case) did not confer additional suppression beyond that already associated with temporal predictability. For this reason, the reduction in N1 and P2 amplitudes for stimuli that were made temporally-predictable does not appear to reflect specific predictions regarding the nature of a stimulus as much as a general expectation that *something* will occur.

We have proposed that the reduction in P2 amplitudes associated with temporal predictability may be reflective of heightened attentional control. This finding may need to be reconciled, however, with previous research that has observed enhanced N1 amplitudes when participants are oriented to the timing of specific stimuli. In their examination of the effects of temporal orienting, Lange et al. (2003) required participants to respond to tones that were separated by either a short interval (i.e., 600 ms) or long interval (i.e., 1200 ms) in intermixed sequences of auditory stimuli. Specifically, participants were asked to respond to tones that deviated from others on the basis of stimulus intensity. Lange et al. (2003) observed enhanced N1 amplitudes to stimuli in target windows (i.e., those in which stimuli would inform participant responses, based on the interval separating a stimulus from the preceding trial). While Lange et al. (2003) attributed this enhancement to the effects of heightened attention during target windows, temporal predictability has been associated with reduced N1 amplitudes in the present findings and previous literature (Lange, 2009; Schafer & Marcus, 1973; Schwartze et al., 2011; Sowman et al., 2012; Vroomen & Stekelenburg, 2010; Weiskrantz et al., 1971). We have also observed evidence of heightened attentional control for such stimuli, which we propose is reflected in P2 amplitudes. While further research is needed, task relevance may serve to account for these apparent discrepancies. In particular, attentional control may facilitate suppressed N1 amplitudes to temporally-predictable stimuli when the characteristics of a stimulus (e.g., tone frequency or intensity) are not task relevant, while higher levels of attention may facilitate an enhanced response when they are. This may account for enhanced N1 amplitudes based on temporal orienting in the experiment by Lange et al. (2003), which required participants to respond based on the properties of sound stimuli, and suppressed N1 amplitudes in our own findings.

6.2.2 Temporal control

An individual’s capacity to determine the timing of self-generated stimuli has also been identified as a potential confound to research examining sensory attenuation (see Hughes et al., 2013a; Hughes et al., 2013b). As an individual must contribute in some way to the production of a stimulus in order to exert control over its timing, externally-generated stimuli are not typically subject to temporal control. In contrast, the timing of self-generated stimuli may be controlled by an individual or this may be determined by external cues to which they respond. In the sensory attenuation literature that has examined the processing of stimuli resulting from self-paced action, the potential influence of temporal control is not able to be separated from participants’ input to the production of stimuli per se. For this reason, the effects of temporal control were explored across each study in the present body of work with a view to understanding related effects and their influence on the phenomenon of sensory attenuation.

In each experiment, the effects of temporal control were assessed through comparison of ERPs resulting from stimuli that were produced by uncued (i.e., self-paced/volitional) action with those elicited by cued (i.e., stimulus-driven) action. In Studies 1 and 2, stimuli resulting from uncued action were found to elicit smaller N1 amplitudes compared with those resulting from action that was cued using the ‘ticker-tape’ visual stimuli. While research into the effects of temporal control remains limited, this result may be consistent with findings from the investigation by Weiss et al. (2011). In their study, the perceived loudness of sounds elicited by self-generated stimuli was less when these were produced in response to an experimenter’s prompts than when self-paced. While this effect was attributed by Weiss et al. (2011) to the influence of social interaction on perceptions of agency and associated sensory attenuation, our results may reflect a more generalised influence. That is, our findings suggest that the effect of a reduction in temporal control may be observed in the absence of another agent to which the timing may be attributed.

In Study 1, we found that the magnitude of the effect of temporal control on N1 amplitudes was such that sensory attenuation was diminished for stimuli resulting from uncued action. The potential role of action-effect contingency was explored in Study 2, by comparing ERPs to self-generated tones that also differed with respect to whether sound stimuli may be reliably predicted (i.e., 100% versus 50% likelihood of a resulting tone). Bayesian analyses provided substantial evidence that action-effect contingency did not differentially affect N1 amplitudes resulting from stimuli that were generated by each form of action. These results suggest that the effect of temporal control on N1 amplitudes does not involve mechanisms that are reliant on action-effect prediction, including those contained within the IFM.

Evidence was provided in Study 4 that the effect of temporal control may be influenced by the interval between stimuli. In particular, an interaction was observed between *ITI* (i.e., representing a median split by participant and condition based on the intervals between trials) and *volition* (i.e., representing the difference between stimuli resulting from cued and uncued action). N1 amplitudes elicited by stimuli that resulted from volitional (i.e., uncued) action, over which participants had temporal control, were found to be increased for trials involving shorter intervals. At the same time, N1 amplitudes were not found to differ based on ITI for stimuli resulting from cued action, over which participants did not have temporal control. Interestingly, an interaction was also observed between *ITI* and *self-generation* (i.e., representing the difference between stimuli that were externally-generated and those produced by either cued or uncued action). Shorter ITIs were found to be associated with smaller N1 amplitudes for externally-generated stimuli, compared with those of self-generated stimuli. These findings may suggest that the effect of temporal control operates on a continuum, whereby uncued action is associated with the greatest level of temporal control while cued action involves a level that is part-way between uncued action and externally-generated events.

By demonstrating that N1 amplitudes are influenced by temporal control, our findings highlight the importance of accounting for this effect in research exploring sensory attenuation. In literature that has compared self-generated stimuli produced through uncued action with that of externally-generated events, the effects of temporal control may contribute to an underestimation of sensory attenuation. For these reasons, future research into sensory attenuation may attempt to minimise the potential influence of temporal control through such methods as we have employed here. As the results of Study 4 indicate that effects involving temporal control are not entirely diminished for cued action, alternate methodological approaches (e.g., use of transcranial magnetic stimulation [TMS]) may need to be explored. For example, future research may compare the effects of externally-generated stimuli with those resulting from movement that is initiated through TMS.

6.2.3 Action-effect prediction

The internal forward model of sensory attenuation suggests that suppression of self-generated sensations, relative to those produced externally, is reliant on predictions that are derived from the motor commands through which they are produced (Miall & Wolpert, 1996; Wolpert et al., 1995). As sensory attenuation has often been studied through examination of the N1 component, this feature of the neurophysiological response should be sensitive to action-effect prediction (i.e., the likelihood of an action eliciting a specific stimulus). However, our findings suggest that this may not be the case. In particular, Studies 2 and 3 specifically examined the influence of action-effect prediction on the evoked response to self-generated tones. Bayesian analyses in Study 2 suggested that action-effect contingency (i.e., comparing action that was associated with 100% likelihood of eliciting a tone with those involving 50% likelihood) did not influence the amplitudes of resulting N1 components. This was the case for stimuli resulting from both volitional (i.e., uncued) and stimulus-driven (i.e., cued) action. These findings suggest that N1 amplitudes are not sensitive to the predictability of self-generated stimuli.

Study 3 examined the interaction between self-generation and stimulus predictability (i.e., involving sequences with consistent presentation of the same tone frequency or two intermixed tone frequencies). While smaller N1 amplitudes were observed for tones contained in sequences with a single frequency, Bayesian analyses indicated substantial evidence that the effect of sequence (i.e., reflecting tone frequency prediction) did not differ between self- and externally-generated tones. Similarly, our analyses indicated that the effect of sequence did not differ on the basis of temporal predictability (i.e., contrasting *uncued listening* and *cued listening* conditions). For this reason, our findings may reflect habituation to specific tone frequencies in a manner consistent with repetition suppression (see Desimone, 1996) for both self- and externally-generated sequences. As with Study 2, the predictability of stimuli based on the motor commands used in their production did not appear to influence N1 amplitudes. It is worth noting, however, that this conclusion may be limited by assumptions with respect to the additivity of prediction-related effects. As recent evidence has suggested that repetition suppression may be the result of increased stimulus predictability over successive exposures (Auksztulewicz & Friston, 2016; Mayrhauser et al., 2014; Summerfield et al., 2008), any conclusions with respect to the effects of motor-based predictions are limited by the assumption that the influence of repetition and motor predictions are additive.

Our findings are in contrast with previous literature suggesting that sensory attenuation is directly influenced by action-effect prediction (e.g., Bäß et al., 2008; Hughes et al., 2013a). In their experiment, Bäß et al. (2008) compared N1 amplitudes to self- and externally-generated sound in sequences containing a single tone frequency or random variation in tone frequencies (i.e., representing predictable and unpredictable stimuli, respectively). Their findings indicated that sensory attenuation was largest when comparing stimuli produced in sequences with a tone frequency, potentially reflecting the operation of IFM-based prediction (i.e., on the basis of motor commands). However, the results of this study were limited by the presentation of separate blocks including combinations of self-generated, externally-generated, predictable and unpredictable stimuli. For this reason, interactions between predictability and self-generation may be attributable to such factors as arousal and attention, rather than necessarily entailing motor-based prediction.

An experiment by Hughes et al. (2013a) compared the amplitudes of auditory N1 components that were elicited by self-generated tones in intermixed trials that differed with respect to action-effect predictability. Participants produced either low- or high-pitch tones by pressing one of four different keys involving two fingers on each hand (see Fig. 6.1). One finger on each hand had 100% likelihood of producing a particular frequency (e.g., high pitch), while the other finger had a 50% likelihood of a high-pitch tone and a 50% likelihood of a low-pitch tone. These stimuli were regarded as predictable and unpredictable, respectively. Allocation of tone frequency was balanced such that the 100% likelihood condition elicited low-pitch tones on one hand and high-pitch tones on the other. As an equal number of predictable and unpredictable trials were included, each hand had an overall likelihood of producing one specific tone frequency 75% of the time (i.e., 100% of predictable trials and 50% of unpredictable trials) and the other frequency 25% of the time (i.e., 50% of unpredictable trials).

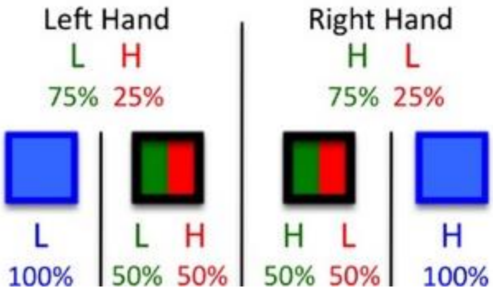


Fig. 6.1. Action-effect contingency in the experiment by Hughes et al. (2013a). In this example, button presses with one finger of the left hand resulted in low-pitch tones 100% of the time, while presses with a second finger had 50% probability of eliciting a low-pitch tone and 50% probability of eliciting a high-pitch tone. Button presses with one finger of the right hand elicited high-pitch tones 100% of the time, while presses with a second finger had 50% probability of eliciting a low-pitch tone and 50% probability of eliciting a high pitch tone. Overall, left hand button presses were associated with 75% probability of eliciting low-pitch tones and 25% probability of eliciting high-pitch tones. Right hand button presses were associated with inverse probabilities. The allocation of tone frequencies to left and right hands were counterbalanced across participants. Adapted from Hughes et al. (2013a).

Significantly, Hughes et al. (2013a) identified that the predictability of stimuli (i.e., contrasting those resulting from key presses with fingers involving 100% likelihood of eliciting a specific tone with those involving 50% likelihood) did not influence the amplitude of resulting N1 components. Instead, they observed that 'hand-specific prediction' (i.e., congruence between a specific stimulus and the *overall* likelihood of either finger on one hand eliciting that tone) resulted in reduced N1 component amplitudes. Hughes et al. (2013a) suggest that this outcome may reflect the hierarchical nature of motor commands (see Jing & Weiss, 2001), such that preparation of movement involving a specific hand supersedes that of a specific finger. In Study 2, button presses were made with participants' left or right hands and were associated with either a 100% likelihood of eliciting sound stimuli or 50% likelihood. As N1 amplitudes were not found to differ between these conditions, the findings of Hughes et al. (2013a) may point to more generalised mechanisms influencing the relationship between action-effect prediction and primary cortical response. This may include, for example, suppressive attentional factors such as those potentially reflected within the LEP and LPP of Study 2 (see discussion in the context of *Attention*, below).

Our results appear to contribute to a growing body of research suggesting that action-effect prediction does not directly influence N1 component amplitudes (Dogge et al., 2019). For example, a recent study by Darriba et al. (2021) involved comparison of N1 amplitudes elicited by the final self-generated tone of two possible four-tone sequences. These stimuli differed with respect to sensory prediction (i.e., based on preceding tones in the sequence) and established action-effect predictions (i.e., based on training blocks in which participants learned to associate specific actions with a given stimulus). Their results indicated that, while the amplitude of N1 components was reduced for stimuli that were congruent with action-effect predictions, sensory predictions resulted in a similar level of suppression. In accordance with results of Study 3, Darriba et al. (2021) noted that differences based on action-effect predictability were observed only at the later stages of sensory processing. Together, these findings highlight the need for further research into the mechanisms underlying sensory attenuation, including potential reconsideration or elaboration of mechanisms proposed by the IFM framework.

6.2.4 Attention

Our results provide several indications that attentional effects may contribute to the sensory attenuation phenomenon. Firstly, lateralised activity observed in Study 2 (i.e., the LPP), and a corresponding negativity that spanned the N1 and P2 range, were reminiscent of components known to reflect attentional mechanisms. Significantly, the topography of the LPP closely resembled that of the Pd (i.e., maximal effect when taken as the difference between PO7 and PO8). Research has demonstrated that the Pd may be elicited in response to the involuntary capture of visuospatial attention (Sawaki & Luck, 2013). In closely approximating the timing of the N1, the LPP may therefore reflect activity to suppress attention to spatially-oriented stimuli resulting from movement. That is, congruence between the spatial orientation of motor-related attention and resulting stimuli may support the suppression of self-generated sensations. This notion might serve to reconcile our findings with those of Hughes et al. (2013a), in that ‘hand-specific predictions’ represented the effects of spatial orientation to specific stimuli. As deviant stimuli (i.e., those resulting from button presses with one hand 25% of the time) were oriented to action involving the other hand (i.e., from which they resulted 75% of the time), attentional suppression of resulting stimuli may have been reduced. Future research may therefore examine potential effects involving the spatial orientation to self-generated sensations and resulting neurophysiological response.

Secondly, self-generated stimuli were found to produce significantly smaller P2 amplitudes (i.e., independently of N1 effects) compared to those resulting from externally-generated events in Study 3. Although the functional properties of the P2 remain relatively poorly understood, several lines of evidence have implicated the component in attentional processes. In addition to the Nd/‘processing negativity’ effect (Hillyard et al., 1973), attention-related suppression of the P2 has been observed independently of the N1 in a manner that has been attributed to task relevance (García-Larrea et al., 1992; Novak et al., 1992) and alertness (Colrain et al., 2000). Specifically, it has been proposed that suppression of the P2 may reflect an executive control process supporting withdrawal of attention from non-relevant stimuli (García-Larrea et al., 1992). Reduced P2 amplitude for self-generated stimuli may therefore provide further evidence that these stimuli were subject to heightened attentional control compared with levels allocated to those produced by externally-generated events.

Several previous studies have attempted to evaluate the influence of attentional factors on the phenomenon of sensory attenuation. For example, Timm et al. (2013) manipulated attention to self-generated tones by requiring participants to count events relating to tones, motor action or visual stimuli. Each block in their experiment included motor action that elicited tones, motor action without resulting tones, externally-produced tones and transient variation in the fixation cross on which participants focussed. Timm et al. (2013) observed that, despite attention-related enhancement when participants attended to tones, the amplitude of auditory N1 components elicited by self-generated tones remained significantly smaller than those that were externally-generated. However, it is noteworthy that externally-generated tones were not temporally predictable and therefore subject the methodological limitations we have highlighted above. For this reason, I suggest that these findings do not preclude the role of attention in sensory attenuation.

An investigation by Saupe et al. (2013) explored the effect of increasing participant attention to temporal patterns in passively observed stimuli, in a similar manner to the requirements of uncued self-generation. In the self-generation condition, participants were required to vary the intervals in a sequence of button presses to produce self-generated tones. In a 'passive listening' condition, participants were instructed to simply listen to this sequence of tones, while an 'active listening' condition asked participants to detect intervals that were particularly short (i.e., <1.8 secs) or long (i.e., >5 secs). Saupe et al. (2013) observed an increase in the amplitude of N1 components elicited by tones in the active listening condition, compared with those that were passively observed, in a manner consistent with increased attention to auditory stimuli. While they propose that these findings indicate that sensory attenuation may be sensitive to changes in attention, Saupe et al. (2013) suggest that topographical differences between effects involving attention and sensory attenuation point to differing neural mechanisms. Alternatively, this may be consistent with the results of Study 4 by reflecting differences in the interaction between non-motor identity prediction and attention.

Interesting findings by Cao and Gross (2015) may also support the notion that sensory attenuation is associated with attentional factors. In their study, participants were required to detect near-threshold target tones that were either self-generated or produced externally. Each trial involved one of three different tone frequencies, which varied randomly and were therefore not predictable to participants. Signal detection theory (see Stanislaw & Todorov, 1999) was used to compare participants' accuracy in the detection of the target and non-target tones. In accordance with previous findings (Borra et al., 2013; Greenberg & Larkin, 1968), target tones were found to be detected more accurately than non-target tones. This effect has previously been attributed to attentional differences, whereby target tones are more highly attended than non-target tones (Borra et al., 2013; Greenberg & Larkin, 1968). Interestingly, Cao and Gross (2015) observed a significant interaction such that attentional effects were attenuated with respect to self-generated tones. In particular, target (i.e., attended) tones were less accurately detected when they had been self-generated compared with those produced externally. This finding may therefore also be consistent with the notion that sensory attenuation involves suppressed attention to self-generated sensations.

6.3 Distinguishing volitional and stimulus-driven movement

In addition to supporting an improved understanding of mechanisms underlying sensory attenuation, the present research has important implications for other aspects of sensorimotor integration. Specifically, our findings have demonstrated consistent differences in the sensory processing of stimuli that result from volitional and stimulus-driven actions. Besides the primary cortical response, which we have discussed in the context of sensory attenuation, these relate to such functions as attentional control and error monitoring. Our findings may therefore provide insight into the nature of a broader range of sensorimotor processes and serve to highlight the importance of distinguishing mechanisms involved in each form of movement. In the following section, I provide a summary and synthesis of findings in this regard.

Attentional differences relating to stimulus-driven and volitional movement were indicated in effects involving lateralised activity at the moment of enactment and shortly following (i.e., the LEP and LPP), as well as the N1. As discussed, Study 2 revealed significant differences in lateralised activity that we propose may reflect processes associated with the termination of attention involved in the generation of movement and suppression of attentional capture by resulting stimuli. The magnitude of this lateralised activity differed between stimulus-driven action and volitional movement, corresponding to differences in the amplitude of resulting N1 component amplitudes (i.e., relative suppression of those elicited by stimuli produced through stimulus-driven movement). The nature of this difference, which spanned the N1 and P2 component latencies, also appeared consistent with the Nd wave associated with attentional effects (see Hillyard et al., 1973).

Another key finding with respect to sensorimotor processes in stimulus-driven and volitional movement pertains to differences in error monitoring. In Study 3, examination of N2b component amplitudes revealed an interaction between the form of action (i.e., stimulus-driven versus volitional movement) and stimulus predictability (i.e., whether action consistently produced the same tone frequency or one of two different tone frequencies in an unpredictable manner). In particular, unpredictable tones resulting from volitional movement were associated with increased N2b component amplitudes, while these did not differ on the basis of the predictability of tone frequencies for stimulus-driven movement. Given that the N2b component is elicited in response to action-related error (Ferdinand et al., 2008; Folstein & Van Petten, 2008), this finding appears to reflect monitoring of the sensory results of volitional movement that is absent with regard to stimulus-driven activity. This may suggest that random variation in the frequency of tones across sequential trials appears to contribute to the generation of action-effect predictions which, when violated, elicit N2b responses. In contrast, N2b component amplitudes were not found to differ for tones contained in sequences of predictable and unpredictable frequencies. This may suggest that either predictions were not developed on the basis of action-effects or that the outcomes of each movement were not monitored against such predictions. Taken together, our findings suggest that sounds produced through stimulus-driven action may receive less attention and are not subject to comparison with action-effect predictions in the same manner as the outcomes of volitional movement.

6.4 Agency and control

Ideomotor theory (James, 1890) proposes that movement is selected on the basis of its capacity to achieve intended outcomes, suggesting that our predictions are implicit to the generation of motor activity (see Shin et al., 2010). By facilitating comparison of observed sensory outcomes with those that are predicted on the basis of specific motor commands, the

IFM is believed to contribute to processes involved in the initiation and dynamic coordination of movement (Hommel et al., 2001; Prinz, 1990; Prinz, 1997; Wolpert et al., 1995). Through comparison of the intended and observed outcomes to movement, mechanisms of the IFM are also believed to subserve one's sense of agency over sensation (Blakemore et al., 2002; Wolpert & Ghahramani, 2000). Because the predicted effects of movement also represent one's intentions, the level of discrepancy between predicted and observed outcomes is believed to be inversely associated with one's perception of agency (see Haggard, 2017).

As a phenomenon that has been attributed to action-effect prediction within the IFM, sensory attenuation has been a focus of research seeking to explore agency and control. In particular, higher levels of sensory attenuation have been interpreted to reflect increased agency over associated sensation. However, our findings in relation to the mechanisms of sensory attenuation may warrant caution with regard to this interpretation. Specifically, the results of Studies 2 and 3 suggest that action-effect prediction does not influence primary cortical response (i.e., N1 amplitude). Instead, we have explored evidence that attentional mechanisms may underly a reduction in the primary cortical response for some forms of self-generated stimuli relative to those produced by externally-generated events. This effect appears to be specific to stimuli produced through cued (i.e., stimulus-driven) action conducted in short succession and to derive from attentional mechanisms rather than action-effect prediction.

In contrast to the notion that agency is associated with an attenuation of the primary cortical response, results from our investigations suggest that it may in fact be associated with larger N1 amplitudes. In Study 1, we observed that stimuli resulting from self-paced (i.e., uncued/volitional) action elicited larger N1 amplitudes than those produced by stimulus-driven action. This effect was found to be increased for self-generated stimuli separated by shorter intervals in Study 4. The interaction between ITI and volition (i.e., contrasting stimulus-driven and volitional movement) was found to result from increased enhancement of N1 amplitudes when resulting from uncued action that were separated by shorter intervals. In contrast, we observed a reduction in N1 amplitudes elicited by externally-generated stimuli for trials that were separated by shorter intervals in a manner consistent with the effects of repetition suppression (see Desimone, 1996). The magnitude of these effects was such that a reversal of the sensory attenuation phenomenon was observed for stimuli resulting from volitional action produced in short succession.

While further research is needed, findings with respect to the P50 component in Study 4 may provide an important clue to the nature of differences in the N1 amplitude for stimuli produced by cued (i.e., stimulus-driven) and uncued (i.e., volitional) action. Previous literature has observed a reduction in the P50 amplitude elicited by sound that follows an identical stimulus in short succession (e.g., Fruhstorfer et al., 1970; Nagamoto et al., 1989). This effect has been attributed to ‘sensory gating’, whereby extraneous or irrelevant sensory information is blocked from further processing at a stage that precedes attentional influence (Pratt et al., 2008). In other words, sensory gating represents one’s preparedness to admit sensory information for processing and occurs prior to effects associated with attention. In Study 4, we observed smaller P50 components in response to sequences of stimuli that were produced by uncued action compared with those resulting from cued action, suggesting that stimuli produced by uncued action were subject to higher levels of sensory gating. At the same time, we observed evidence that these stimuli may have been subject to higher levels of attention.

On the basis of documented effects involving repetition suppression and non-motor identity prediction, our findings may support the attribution of ‘volitional enhancement’ to attentional mechanisms. We have previously cited research suggesting that the reduced cortical response observed in repetition suppression may be attributable to effects involving heightened stimulus predictability over successive exposures (Auksztulewicz & Friston, 2016; Mayrhauser et al., 2014; Summerfield et al., 2008). That is, the magnitude of cortical response may decrease as an observer becomes more familiar with the characteristics of repeated stimuli. Significantly, prediction-based suppression of cortical response has been found to be reversed for stimuli that are subject to higher levels of attention (Kok et al., 2012). In light of these findings, our results may be consistent with a reversal of the effects of repetition suppression through higher levels of attention to stimuli produced by volitional movement.

6.5 Clinical implications

A large body of evidence has identified deficits in sensory attenuation among people with schizophrenia (Blakemore et al., 2000; Ford et al., 2012; Ford & Mathalon, 2005; Ford & Mathalon, 2012; Ford, Mathalon, Kalba, et al., 2001; Ford et al., 2014; Ford, Roach, et al., 2007; Heinks-Maldonado et al., 2007; Whitford et al., 2011). This has included research exploring differences in the subjective experience of sensation, such as increased ticklishness of self-generated tactile stimulation (e.g., Blakemore et al., 2000), and neurophysiological measures such as the N1 (e.g., Ford & Mathalon, 2012; Ford, Mathalon, Kalba, et al., 2001; Ford et al., 2014; Heinks-Maldonado et al., 2007; Whitford et al., 2011). Such findings have previously been attributed to dysfunction in IFM mechanisms, whereby corollary discharge is not able to be used to facilitate the prediction and therefore suppression of sensations resulting from movement (Feinberg & Guazzelli, 1999). However, results of the current investigation appear to implicate attentional mechanisms in the sensory attenuation phenomenon. In so doing, our findings may serve to coalesce theories emphasising the role of attention deficits associated with schizophrenia and observed differences in the sensory processing of self- and externally-generated sensations.

In addition to the hallmark symptoms of hallucinations and delusions (i.e., positive symptoms), schizophrenia is associated with impairments to such basic cognitive processes as attention and memory (Green, 1998; Keefe & Harvey, 2012). Interestingly, evidence suggests that these cognitive deficits more accurately predict long-term outcomes than do positive symptoms (Tandon et al., 2010). Luck et al. (2019) recently proposed an overarching framework to account for the cognitive dysfunction experienced by people with schizophrenia. This *hyperfocusing* account postulates that people with schizophrenia apply an abnormally narrow but intense focus of processing resources. Such narrow focus is believed to contribute to difficulties distributing attention among multiple locations, maintaining several representations in working memory and, significantly, resisting attentional capture by irrelevant stimuli. Findings from Sawaki et al. (2017) provide key evidence in support of this notion, demonstrating that people with schizophrenia exhibit reduced Pd component amplitudes in response to distractor visual stimuli compared with healthy controls. This suggests that people with schizophrenia experience difficulty suppressing attentional capture. In contrast, differences were not observed in the magnitude of the N2pc component, indicating that selective attentional abilities do not differ between healthy individuals and people with schizophrenia. Study 2 suggested that sensory attenuation may be associated with the suppression of attentional capture by stimuli resulting from action, based on lateralised activity that was similar to the Pd component (i.e., which we have described as the LPP). Deficits in sensory attenuation among people with schizophrenia may therefore be reflect diminished capacity to suppress, through attentional mechanisms, self-generated sensations.

Recent research has indicated that, in addition to overt stimuli, sensory attenuation may be observed in association with the production of imagery (Ford & Mathalon, 2004; Ford, Mathalon, Kalba, et al., 2001; Ford, Mathalon, Theda, et al., 2001; Whitford et al., 2017). In a recent investigation, Whitford et al. (2017) found that the auditory N1 amplitudes elicited by phonemes were suppressed when these were congruent with the contents of inner speech, relative to those that were incongruent or passively observed (i.e., without simultaneous production of inner speech). This finding may suggest that imagery is subject to sensory attenuation in a similar way to overt stimuli, facilitating a distinction between imagined and externally-generated sensations. In conjunction with evidence that schizophrenia is associated with deficits in sensory attenuation, this finding may support the notion that hallucinations represent a misattribution of imagery to external sources such that they are experienced as overt perception (Feinberg, 1978). Findings from the present investigation may suggest that the underlying mechanism involves a deficit in the suppression of attention to imagery.

6.6 Limitations and future research

The current body of work has several potential limitations that should be considered. Firstly, effects relating to sensory attenuation have been explored through examination of factors influencing the amplitude of auditory N1 components. This was in accordance with previous electrophysiological investigations of sensory attenuation. However, the phenomenon has been explored across a variety of methodological approaches including other neuroimaging techniques, such as fMRI for example, and subjective report. While the auditory N1 is known to reflect activation within the primary auditory cortex (Giard et al., 1994; Näätänen & Picton, 1987; Zouridakis et al., 1998), and is influenced by stimulus intensity (i.e., the loudness of sound; Mulert et al., 2005), further research is needed to explore the relationship between effects we have observed and the subjective intensity of sensation and other neuroimaging markers. This may consider effects relating to the Tb component, for example, given recent evidence reflecting its sensitivity to agency over the production of sound stimuli (Han et al., 2021; Han et al., 2022). Conclusions are therefore limited regarding the generalisability of our findings to research that has explored sensory attenuation through such alternative indices, which may warrant future investigation.

The generalisability of our findings is also limited with respect to action-effect predictions that are acquired over a longer duration than was included in the experimental procedures. That is, our conclusions have assumed that effects relating to motor predictions may be developed and identified based on learning that occurs over the duration of the experiment. I acknowledge that the entrenchment of associations that have been learned over a lifetime of exposure (e.g., the sound of one's own vocalisations, the tactile sensation of self-touch, or proprioception) may result in effects not able to be observed in the present investigation. While much of the sensory experience that we produce while navigating our surrounds is regularly changing (e.g., the sound of one's footsteps on different surfaces or tapping our finger against different objects), further research is needed to investigate the potential that motor-based predictions involving more deeply ingrained action-effect associations contribute to differing outcomes. A distinction between speech and non-speech stimuli may be particularly informative, given the wealth of research demonstrating sensory attenuation of speech stimuli during vocalisation (e.g., Creutzfeldt et al., 1989; Curio et al., 2000; Ford, Mathalon, Kalba, et al., 2001) and evidence of similar effects resulting from speech imagery (Whitford et al., 2017). More generally, it has been recently argued that the distinction between body-related and environment-related outcomes to movement is particularly important, including with respect to both motor control (Pfister, 2019) and sensory processing (Dogge et al., 2019). This distinction presents an important avenue for future research, including with respect to whether the use of body-related and environment-related action effects differs innately or as a function of how deeply these associations are learned.

Moreover, we have assessed effects involving volition based on a simple distinction between movement that is self-paced and produced in response to simple visual cues. Observed differences reflect effects associated with constraint over the timing of action, which may inadequately capture effects involving volition. Firstly, it is not true to say that cued action did not involve some level of agency with respect to when participants respond, or that uncued action allowed participants to respond without any constraint on timing. In this respect, our manipulation represents a comparison between action involving a larger degree of control over the timing of stimuli with those involving less. Secondly, the action required from participants in any given trial was subject to experimental demands rather than participant choice (i.e., they were told which key to press). In this sense, participants did not have agency over the type of action they produced and our results are not able to speak to associated effects. Future research may explore differences associated with the degree and nature of volition in movement. This may be achieved, for example, through comparison of sensory processing when stimuli are produced by volitional movement with those resulting from action elicited by TMS. Through direct stimulation of the motor cortex, such methods may facilitate the production of movement without conscious intent to more fully isolate effects associated with volitional action.

Finally, future research may also seek to address limitations regarding the manner in which motor effects were corrected in the present body of work. Recent research has indicated that participants may adjust their motor actions based on the contingency of resulting effects (i.e., whether they anticipate that the movement will elicit a tone or not; Horváth et al., 2018). It is possible that such differences may have affected the accuracy with which motor activity was corrected in the present body of work, which would have implications for the comparison of neurophysiological responses to self- and externally-generated stimuli. Similarly, if the discrepancy between motor-stimulus and motor conditions differed between volitional and stimulus-driven movement, this may present a potential confound to the comparison of stimulus-processing for each form of action. Future research may be needed to validate the present findings using apparatus capable of measuring response force and duration, or other methods to control for motor activity associated with each form of action.

6.7 Conclusion

The series of experiments that constituted this thesis have explored factors affecting the production and processing of self-generated stimuli compared with those produced externally. Through carefully controlled paradigms, we have evaluated key assumptions of the IFM framework while addressing previous experimental confounds. Our results have highlighted a range of factors influencing the auditory N1 and the importance of controlling for these in research seeking to explore sensory attenuation. In particular, we have found evidence to suggest that temporal predictability and temporal control have opposing effects on the amplitude of auditory N1 components. While temporal predictability is associated with a suppression of N1 amplitudes, temporal control appears to result in an amplification. In addition, we have described an interaction between the effect of temporal control and the interval between stimuli such that the effect of sensory attenuation may be countervailed with respect to those produced in short success.

Contrary to the notion that sensory attenuation is facilitated by the prediction of self-generated stimuli based on the motor commands through which they are produced, our findings appear to implicate suppressive attentional factors. These were evidenced by lateralised activity that was consistent with the Pd component, reflecting the suppression of spatially-oriented attention, that coincided with a suppression of sensory processing in the primary auditory cortex (i.e., the auditory N1). This finding may suggest that sensory attenuation involves the suppression of self-generated sensation based on attentional mechanisms. Findings with respect to the P2 also reflect differences in attentional control, such that attention to self-generated sensations may be more easily terminated. While further research is needed, these findings may cast doubt on several foundational features of the IFM framework of sensorimotor processing and may warrant reconsideration of associated theory. The preliminary evidence that we have explored in support of alternative accounts of sensory attenuation, including those favouring attentional mechanisms, may have wide-ranging implications. Caution is warranted, however, until such time as these results are replicated and research has thoroughly explored other aspects of motor-based prediction, including those discussed in the context of findings by Hughes et al. (2013a).

In addition, our findings have highlighted differences in the processing of stimuli that result from volitional (i.e., uncued) and stimulus-driven (i.e., cued) movement in a manner that is consistent with the predictions of ideomotor theory. Differences in N2b component amplitudes were found to reflect comparison of motor-based predictions with stimuli resulting from volitional movement. In contrast, stimuli that resulted from stimulus-driven movement did not appear to be subject to such error monitoring. We have proposed that these findings are consistent with the notion that volitional action involves comparison of the intended and actual outcomes to movement, while stimulus-driven action may be enacted with less regard for its specific sensory effects.

Together, the findings of these investigations provide new insight into the mechanisms underlying sensory attenuation and highlight the importance of distinguishing processes associated with volitional and stimulus-driven movement. In addition to implications regarding normative processing of self-generated sensations, results from the present investigation may serve to inform future research into the aetiological basis of schizophrenia. Recognition of the role of selective attentional mechanisms in sensory attenuation may assist in the integration of observed cognitive impairments with those involving positive symptoms, including hallucinations and delusions. In this way, our findings provide new avenues for research into the neural basis and therapeutic interventions to address abnormal sensory processing in schizophrenia. Ultimately, these developments may aid in progress towards an improved quality of life for those experiencing its effects.

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Appendix 1

Table A1.1

Paired samples Student's t-tests contrasting N1 amplitudes in Experiment 1

Comparator 1	M_1	SD_1	*Comparator 2*	M_2	SD_2	*df*	M_{diff}	*t*	*p*	p_{corr}	*d*	BF_{10}
Uncued listening	-3.96	1.78	Cued listening	-3.07	2.24	41	-0.89	-3.46	.001	.003	-0.441	24.542
			Uncued self-generation	-3.22	1.93	41	-0.74	-2.60	.013	.019	-0.400	3.219
			Cued self-generation	-1.91	2.26	41	-2.05	-6.10	<.001	<.001	-1.013	50,782.424
Cued listening	-3.07	2.24	Uncued self-generation	-3.22	1.93	41	0.15	0.47	.639	.639	0.070	0.185
			Cued self-generation	-1.91	2.26	41	-1.16	-2.87	.006	.011	-0.514	5.851
Uncued self-generation	-3.22	1.93	Cued self-generation	-1.91	2.26	41	-1.31	-3.57	<.001	.003	-0.624	32.193

Table A1.2

Paired samples Student's t-tests contrasting P2 amplitudes in Experiment 1

Comparator 1	M_1	SD_1	*Comparator 2*	M_2	SD_2	*df*	M_{diff}	*t*	*p*	p_{corr}	*d*	BF_{10}
Uncued listening	2.18	3.10	Cued listening	2.52	2.94	41	-0.34	-0.81	.423	.462	-0.112	0.227
			Uncued self-generation	-0.14	2.88	41	2.32	4.44	<.001	<.001	0.778	352.033
			Cued self-generation	1.73	2.96	41	0.45	0.86	.394	.472	0.148	0.236
Cued listening	2.52	2.94	Uncued self-generation	-0.14	2.88	41	2.66	4.34	<.001	<.001	0.915	261.992
			Cued self-generation	1.73	2.96	41	0.79	1.57	.124	.165	0.267	0.517
Uncued self-generation	-0.14	2.88	Cued self-generation	1.73	2.96	41	-1.88	-3.46	.001	.003	-0.643	24.313

Table A1.3

Paired samples Student's t-tests contrasting N1 amplitudes in Experiment 2

Comparator 1	M_1	SD_1	*Comparator 2*	M_2	SD_2	*df*	M_{diff}	*t*	*p*	p_{corr}	*d*	BF_{10}
Cued listening	-3.18	1.88	Cued listening (count)	-3.12	2.03	37	-0.06	-0.22	.828	.919	-0.030	0.179
			Uncued self-generation	-3.05	1.61	37	-0.13	-0.33	.746	.933	-0.073	0.184
			Cued self-generation	-2.09	1.89	37	-1.09	-3.08	.004	.023	-0.578	9.343
			Cued self-generation (count)	-2.14	1.57	37	-1.04	-3.09	.004	.029	-0.602	9.496
Cued listening (count)	-3.12	2.03	Uncued self-generation	-3.05	1.61	37	-0.07	-0.16	.873	.903	-0.037	0.177
			Cued self-generation	-2.09	1.89	37	-1.03	-2.85	.007	.031	-0.525	5.555
			Cued self-generation (count)	-2.14	1.57	37	-0.98	-2.47	.018	.055	-0.543	2.499
Uncued self-generation	-3.05	1.61	Cued self-generation	-2.09	1.89	37	-0.96	-2.70	.010	.039	-0.550	4.058
			Cued self-generation (count)	-2.14	1.57	37	-0.91	-3.00	.005	.024	-0.573	7.871
Cued self-generation	-2.09	1.89	Cued self-generation (count)	-2.14	1.57	37	0.05	0.18	.856	.917	0.030	0.177

Table A1.4

Paired samples Student's t-tests contrasting P2 amplitudes in Experiment 2

Comparator 1	M_1	SD_1	*Comparator 2*	M_2	SD_2	*df*	M_{diff}	*t*	*p*	p_{corr}	*d*	BF_{10}
Cued listening	1.89	2.66	Cued listening (count)	1.78	2.53	37	0.11	0.33	.745	.971	0.042	0.184
			Uncued self-generation	-0.24	2.60	37	2.14	4.48	<.001	.002	0.812	346.924
			Cued self-generation	1.19	1.87	37	0.71	1.84	.074	.130	0.312	0.802
			Cued self-generation (count)	0.68	2.29	37	1.21	2.30	.027	.058	0.490	1.786
Cued listening (count)	1.78	2.53	Uncued self-generation	-0.24	2.60	37	2.03	4.17	<.001	.003	0.790	147.793
			Cued self-generation	1.19	1.87	37	0.60	1.80	.081	.135	0.271	0.747
			Cued self-generation (count)	0.68	2.29	37	1.10	2.42	.021	.051	0.457	2.258
Uncued self-generation	-0.24	2.60	Cued self-generation	1.19	1.87	37	-1.43	-3.88	<.001	.004	-0.640	68.552
			Cued self-generation (count)	0.68	2.29	37	-0.93	-1.92	.063	.117	-0.379	0.913
Cued self-generation	1.19	1.87	Cued self-generation (count)	0.68	2.29	37	0.50	1.77	.085	.127	0.243	0.720

Table A1.5

Paired samples Student's t-tests contrasting N2b amplitudes in Experiment 2

Comparator 1	M_1	SD_1	*Comparator 2*	M_2	SD_2	*df*	M_{diff}	*t*	*p*	p_{corr}	*d*	BF_{10}
Cued listening	-0.57	2.58	Cued listening (count)	-1.57	2.81	37	0.99	2.41	.021	.049	0.369	2.203
			Uncued self-generation	-0.61	2.48	37	0.03	0.07	.947	.947	0.013	0.175
			Cued self-generation	-0.75	2.70	37	0.17	0.26	.793	.952	0.066	0.180
			Cued self-generation (count)	-2.23	3.32	37	1.66	2.13	.040	.081	0.563	1.299
Cued listening (count)	-1.57	2.81	Uncued self-generation	-0.61	2.48	37	-0.96	-1.79	.082	.130	-0.364	0.737
			Cued self-generation	-0.75	2.70	37	-0.82	-1.20	.238	.341	-0.298	0.339
			Cued self-generation (count)	-2.23	3.32	37	0.67	0.96	.344	.468	0.218	0.268
Uncued self-generation	-0.61	2.48	Cued self-generation	-0.75	2.70	37	0.14	0.22	.826	.954	0.054	0.179
			Cued self-generation (count)	-2.23	3.32	37	1.63	2.46	.019	.051	0.562	2.445
Cued self-generation	-0.75	2.70	Cued self-generation (count)	-2.23	3.32	37	1.49	2.65	.012	.039	0.495	3.617

1.1 Behavioural data

Experiment 1

Inter-stimulus intervals. Inter-stimulus intervals (ISIs) were analysed to confirm effective and consistent manipulation of timing in conditions involving participant input. Paired samples Student's t-tests were used to compare mean ISIs in *active uncued* and *active cued*, as well as the motor-only conditions used for their correction (i.e., *motor uncued* and *motor cued)*. The mean ISIs (ms) of the *active uncued* condition (M = 2,618.60, SD = 486.27) were not found to differ significantly from those of the *active cued* condition (M = 2,621.48, SD = 489.24), $t(41) = 0.65$, $p = 0.517$, $BF_{10} = 0.20$, or *motor uncued* condition (M = 2,660.31, SD = 495.89), $t(41) = 1.42$, $p = 0.162$, $BF_{10} = 0.43$. Similarly, mean ISIs (ms) of the *active cued* condition were not found to differ significantly differ significantly from the *motor cued* condition, $t(41) = 1.06$, $p = .229$, $BF_{10} = 0.28$.

Experiment 2

Key-press accuracy. A series of paired samples Student's t-test were again used to compare participants' accuracy in pressing the key to synchronise with visual stimuli in the three cued conditions. Results suggested that mean error (ms; i.e., averaged across all trials for each participant) in the *active cued* condition ($M = -72.14$, $SD = 42.44$, $max = 84.06$) did not differ significantly from the *motor cued* condition ($M = -76.76$, $SD = 44.02$, $max = 79.25$), $t(37) = 1.46$, $p = 0.153$, $BF_{10} = 0.461$, or the *active cued (count)* condition ($M = -65.13$, $SD = 40.01$, $max = 79.25$), $t(37) = 1.46$, $p = 0.153$, $BF_{10} = 0.461$. Similarly, the *active cued (count)* condition did not differ significantly from the *motor cued* condition, $t(37) = 1.69$, $p = .100$, $BF_{10} = 0.636$.

Inter-stimulus intervals. Manipulation of timing in conditions involving participant action was again evaluated. A series of paired samples Student's t-tests were used to compare mean ISIs in *active uncued*, *active cued* and *active cued (count),* as well as their motor-only controls (*motor uncued* and *motor cued)*. Mean ISIs (ms) did not differ significantly between the *active uncued* condition (*M* = 2,421.38, *SD* = 393.11) and the *motor uncued* condition (*M* = 2,491.7, *SD* = 508.83), *t*(37) = 1.54, *p* = 0.133, BF_{10} = 0.51. Mean ISIs were also not found to differ significantly between *active uncued* and *active cued* (*M* = 2,420.71, *SD* = 390.1), *t*(37) = 0.27, *p* = 0.786, BF_{10} = 0.18, *active cued (count; M* = 2,423.8, *SD* = 394.26), *t*(37) = 1.54, *p* = 0.138, BF_{10} = 0.50, and *motor cued* (*M* = 2,420.86, *SD* = 390.67), *t*(37) = 0.21, *p* = .835, BF_{10} = 0.18.

Appendix 2

Table A2.1

Readiness potential amplitudes by condition

	Early RP		Late RP		RP	
	M	SD	M	SD	M	SD
Uncued 50% [M-S]	-1.13	1.46	-2.46	2.16	-2.06	1.97
Uncued 50% [M]	-1.30	1.47	-2.38	2.86	-1.98	2.36
Uncued 100% [M-S]	-1.60	1.59	-3.16	2.44	-2.73	2.24
Cued 50% [M-S]	-2.55	2.03	-3.61	3.51	-3.62	2.95
Cued 50% [M]	-2.38	2.01	-3.45	4.16	-3.45	3.46
Cued 100% [M-S]	-3.09	2.31	-4.25	4.30	-4.54	3.66

Table A2.2

Lateralised component amplitudes by condition

	LRP		LEP		LPP	
	M	SD	M	SD	M	SD
Uncued 50% [M-S]	-1.51	2.12	0.90	1.34	-0.44	2.38
Uncued 50% [M]	-1.53	2.11	1.01	1.43	-0.49	2.75
Uncued 100% [M-S]	-1.45	2.51	0.89	1.51	-0.06	1.66
Cued 50% [M-S]	-1.71	2.00	1.37	2.29	0.14	2.86
Cued 50% [M]	-1.37	2.07	1.65	1.78	0.56	2.99
Cued 100% [M-S]	-1.45	2.55	1.91	1.81	1.23	3.93

Table A2.3

Motor-corrected N1 component amplitude by condition

	M	SD
Uncued 50% [M-S]	-4.11	2.05
Uncued 100% [M-S]	-4.11	2.39
Cued 50% [M-S]	-3.47	2.32
Cued 100% [M-S]	-3.54	2.44

Table A2.4

Readiness and lateralized potential ANOVA results

		df_{num}	df_{den}	SS_{num}	SS_{den}	F	p	η_p^2	BF_{10}
Early RP	Intercept	0.98	61.94	1,548.97	675.20	144.53	<.001	0.696	1.00E+00
	Cueing	0.89	56.06	169.60	340.96	31.34	<.001	0.332	2.12E+15
	Contingency	1.97	123.88	21.65	132.36	10.30	<.001	0.141	1.76E+00
	Cueing x Contingency	1.78	112.12	2.99	126.68	1.48	.231	0.023	8.88E-02
Late RP	Intercept	0.91	57.26	3,980.01	2,650.64	94.60	<.001	0.600	1.00E+00
	Cueing	0.94	59.38	115.79	976.91	7.47	.008	0.106	5.01E+03
	Contingency	1.82	114.52	46.65	336.19	8.74	<.001	0.122	1.65E+00
	Cueing x Contingency	1.88	118.75	0.12	253.61	0.03	.971	<.001	5.34E-02
RP	Intercept	0.93	58.86	3,602.86	1,734.47	130.86	<.001	0.675	1.00E+00
	Cueing	0.92	57.89	250.41	786.92	20.05	<.001	0.241	1.67E+10
	Contingency	1.87	117.72	63.39	294.49	13.56	<.001	0.177	1.01E-02
	Cueing x Contingency	1.84	115.78	1.85	243.27	0.48	0.620	0.008	6.21E-02
LRP	Intercept	0.66	41.29	867.72	672.97	81.23	<.001	0.563	1.00E+00
	Cueing	0.82	51.79	0.02	163.50	0.01	.928	<.001	1.16E-01
	Contingency	1.31	82.58	2.13	712.84	0.19	.829	0.003	3.72E-02
	Cueing x Contingency	1.64	103.59	2.13	342.25	0.39	.677	0.006	6.62E-02
LEP	Intercept	0.71	44.90	636.84	188.34	213.03	<.001	0.772	1.00E+00
	Cueing	0.73	46.29	47.76	122.32	24.60	<.001	0.281	3.96E+02

	Contingency	1.43	89.80	4.77	373.65	0.80	.450	0.013	6.09E-02
	Cueing x Contingency	1.47	92.59	5.12	435.49	0.74	.479	0.012	1.14E-01
LPP	Intercept	0.66	41.31	9.54	700.28	0.86	0.358	0.013	1.00E+00
	Cueing	0.72	45.27	91.72	550.88	10.49	0.002	0.143	4.64E+01
	Contingency	1.31	82.62	37.18	992.72	2.36	0.099	0.036	2.87E-01
	Cueing x Contingency	1.44	90.54	8.34	818.96	0.64	0.528	0.010	8.74E-02

Table A2.5

Readiness and lateralized potential contrasts and interactions

				95% *CI*						
		Estimate	*SE*	Lower	Upper	*df*	*t*	*p*	*d*	BF_{10}
Early RP	Probability	0.13	0.07	-0.01	0.27	126	1.84	.069	0.327	1.75E+00
	Action-effect	0.08	0.12	-0.16	0.32	126	0.68	.495	0.100	1.13E-01
	Cueing	-1.33	0.14	-1.60	-1.05	189	-9.44	<.001	-1.373	9.04E+08
	Probability x Cueing	0.08	0.10	-0.12	0.27	189	0.77	.440	0.113	1.30E-01
	Action-effect x Cueing	-0.17	0.17	-0.51	0.17	189	-0.98	.327	-0.175	1.42E-01
Late RP	Probability	0.25	0.11	0.02	0.47	126	2.17	0.032	0.386	7.82E-01
	Action-effect	-0.04	0.20	-0.43	0.35	126	-0.20	0.843	-0.029	1.17E-01
	Cueing	-1.10	0.23	-1.54	-0.65	189	-4.82	<.001	-0.702	1.59E+01
	Probability x Cueing	-0.01	0.16	-0.32	0.31	189	-0.03	0.973	-0.005	1.13E-01
	Action-effect x Cueing	-0.04	0.28	-0.59	0.50	189	-0.15	0.881	-0.027	1.13E-01
RP	Probability	0.24	0.10	0.03	0.44	126	2.27	0.025	0.405	3.53E+00
	Action-effect	-0.04	0.18	-0.40	0.31	126	-0.23	0.820	-0.033	1.20E-01
	Cueing	-1.62	0.21	-2.02	-1.21	189	-7.72	<.001	-1.123	1.83E+05
	Probability x Cueing	0.09	0.15	-0.19	0.38	189	0.64	0.523	0.093	1.24E-01
	Action-effect x Cueing	-0.05	0.26	-0.55	0.46	189	-0.18	0.860	-0.031	1.14E-01
LRP	Probability	-0.02	0.10	-0.23	0.18	126	-0.22	0.828	-0.039	1.19E-01
	Action-effect	0.01	0.18	-0.34	0.37	126	0.07	0.944	0.010	1.31E-01

	Cueing	-0.01	0.17	-0.34	0.31	189	-0.09	0.929	-0.013	1.13E-01
	Probability x Cueing	-0.01	0.12	-0.24	0.22	189	-0.08	0.938	-0.011	1.13E-01
	Action-effect x Cueing	-0.18	0.20	-0.58	0.22	189	-0.89	0.376	-0.158	1.39E-01
LEP	Probability	0.02	0.09	-0.15	0.19	126	0.26	0.799	0.045	1.63E-01
	Action-effect	-0.05	0.15	-0.35	0.24	126	-0.36	0.722	-0.052	1.65E-01
	Cueing	0.71	0.18	0.36	1.05	189	4.02	<.001	0.585	2.39E+02
	Probability x Cueing	-0.16	0.12	-0.40	0.09	189	-1.26	0.211	-0.183	2.34E-01
	Action-effect x Cueing	-0.09	0.21	-0.51	0.33	189	-0.40	0.691	-0.071	1.21E-01
LPP	Probability	-0.13	0.14	-0.41	0.14	126	-0.95	0.343	-0.170	8.58E-01
	Action-effect	0.02	0.24	-0.45	0.50	126	0.10	0.923	0.014	1.28E-01
	Cueing	0.98	0.27	0.44	1.52	189	3.56	<.001	0.518	2.43E+01
	Probability x Cueing	-0.16	0.19	-0.54	0.22	189	-0.82	0.412	-0.120	1.50E-01
	Action-effect x Cueing	-0.23	0.34	-0.89	0.43	189	-0.69	0.492	-0.123	1.38E-01

Table A2.6

Motor-corrected N1 ANOVA results

	df_{num}	df_{den}	SS_{num}	SS_{den}	F	p	η_p^2	BF_{10}
Intercept	1	63	3,705.41	733.78	318.13	<.001	0.835	1.00E+00
Probability	1	63	0.08	345.44	0.01	.904	<.001	1.38E-01
Cueing	1	63	23.39	152.39	9.67	.003	0.133	4.27E+00
Cueing x Probability	1	63	0.09	109.34	0.05	.821	0.001	1.90E-01

Table A2.7

Inter-trial intervals

	Mean ITI (ms)		
Experimental Condition	*M*	*SD*	*Min*
Uncued 100% [M-S]	2,692.60	359.04	2,084.97
Uncued 50% [M-S]	2,716.24	353.48	2,066.05
Uncued 50% [M]	2,705.94	361.10	2,080.05
Uncued 0% [M]	2,776.58	435.02	2,043.95
Cued 100% [M-S]	2,705.86	347.06	2,110.11
Cued 50% [M-S]	2,728.83	344.84	2,085.15
Cued 50% [M]	2,723.26	351.68	2,117.41
Cued 0% [M]	2,741.63	397.13	2,116.48
Total	2,723.87	365.37	2,043.95

Table A2.8

Trial presentation and behavioural exclusions

		Presented Trials		Missed/Incorrect		Completed Trials	
		M	*SD*	*M*	*SD*	*M*	*SD*
Non-lat.	Uncued 100% [M-S]	120.33	2.48	2.92	5.70	117.41	6.31
	Uncued 50% [M-S]	120.34	2.49	3.06	6.51	117.28	7.12
	Uncued 50% [M]	120.08	0.41	2.77	6.49	117.31	6.52
	Uncued 0% [M]	120.00	0.00	3.16	10.47	116.84	10.47
	Cued 100% [M-S]	120.14	2.88	5.77	6.29	114.38	7.11
	Cued 50% [M-S]	119.91	2.80	5.03	6.73	114.88	7.27
	Cued 50% [M]	119.66	1.05	5.33	6.79	114.33	6.92
	Cued 0% [M]	119.70	0.78	4.39	5.63	115.31	5.76
Lat.	Uncued 100% [M-S]	77.89	4.51	1.92	4.14	75.97	5.21
	Uncued 50% [M-S]	78.44	4.88	2.08	4.63	76.36	7.32
	Uncued 50% [M]	80.34	4.29	1.94	4.89	78.41	6.89
	Cued 100% [M-S]	77.78	4.56	3.31	4.33	74.47	5.54
	Cued 50% [M-S]	78.03	5.14	3.34	4.64	74.69	7.33
	Cued 50% [M]	80.00	4.33	3.56	5.20	76.44	7.15

Table A2.9

Artifact rejection and trial averaging

		Rejected Trials			Averaged Trials			
		M	*SD*	%	*M*	*Mdn*	*SD*	*Min*
Non-lat.	Uncued 100% [M-S]	0.20	0.71	0.17	117.20	119.00	6.39	88.00
	Uncued 50% [M-S]	0.13	0.38	0.11	117.16	119.00	7.07	79.00
	Uncued 50% [M]	0.34	1.06	0.29	116.97	119.00	6.58	78.00
	Uncued 0% [M]	0.19	0.63	0.16	116.66	120.00	10.45	41.00
	Cued 100% [M-S]	0.27	0.96	0.23	114.11	116.00	7.28	86.00
	Cued 50% [M-S]	0.13	0.41	0.11	114.75	117.00	7.28	75.00
	Cued 50% [M]	0.25	0.95	0.22	114.08	116.00	6.93	75.00
	Cued 0% [M]	0.22	0.93	0.19	115.09	117.00	5.79	90.00
Lat.	Uncued 100% [M-S]	0.09	0.34	0.12	75.88	76.00	5.21	62.00
	Uncued 50% [M-S]	0.06	0.30	0.08	76.30	77.00	7.34	43.00
	Uncued 50% [M]	0.20	1.15	0.26	78.20	78.00	6.91	45.00
	Cued 100% [M-S]	0.09	0.38	0.13	74.38	75.00	5.54	60.00
	Cued 50% [M-S]	0.08	0.32	0.10	74.61	76.00	7.34	41.00
	Cued 50% [M]	0.20	0.75	0.27	76.23	77.00	7.11	42.00

Table A2.10

Early RP amplitude contrasts

Comparator 1	M_1	SD_1	Comparator 2	M_2	SD_2	*df*	M_{diff}	*t*	*p*	*d*	BF_{10}
Uncued 100% [M-S]	-1.60	1.59	Uncued 50% [M-S]	-1.13	1.46	63	-0.47	-2.26	0.028	-0.310	1.44E+00
	-1.60	1.59	Uncued 50% [M]	-1.30	1.47	63	-0.30	-1.79	0.078	-0.199	6.18E-01
	-1.60	1.59	Cued 100% [M-S]	-3.09	2.31	63	1.48	4.75	0.000	0.762	1.51E+03
	-1.60	1.59	Cued 50% [M-S]	-2.55	2.03	63	0.95	3.25	0.002	0.526	1.50E+01
	-1.60	1.59	Cued 50% [M]	-2.38	2.01	63	0.78	2.84	0.006	0.433	5.34E+00
Uncued 50% [M-S]	-1.13	1.46	Uncued 50% [M]	-1.30	1.47	63	0.17	1.02	0.312	0.114	2.25E-01
	-1.13	1.46	Cued 100% [M-S]	-3.09	2.31	63	1.95	6.74	0.000	1.039	2.05E+06
	-1.13	1.46	Cued 50% [M-S]	-2.55	2.03	63	1.42	5.12	0.000	0.817	5.35E+03
	-1.13	1.46	Cued 50% [M]	-2.38	2.01	63	1.25	4.64	0.000	0.722	1.04E+03
Uncued 50% [M]	-1.30	1.47	Cued 100% [M-S]	-3.09	2.31	63	1.79	6.27	0.000	0.947	3.47E+05
	-1.30	1.47	Cued 50% [M-S]	-2.55	2.03	63	1.25	4.75	0.000	0.719	1.50E+03
	-1.30	1.47	Cued 50% [M]	-2.38	2.01	63	1.08	4.52	0.000	0.623	6.86E+02
Cued 100% [M-S]	-3.09	2.31	Cued 50% [M-S]	-2.55	2.03	63	-0.53	-2.84	0.006	-0.246	5.25E+00
	-3.09	2.31	Cued 50% [M]	-2.38	2.01	63	-0.71	-3.99	0.000	-0.327	1.28E+02
Cued 50% [M-S]	-2.55	2.03	Cued 50% [M]	-2.38	2.01	63	-0.17	-1.05	0.297	-0.086	2.32E-01

Note. Contrasts represent paired samples Student's t-tests.

Table A2.11

Late RP amplitude contrasts

Comparator 1	M_1	SD_1	Comparator 2	M_2	SD_2	*df*	M_{diff}	*t*	*p*	*d*	BF_{10}
Uncued 100% [M-S]	-3.16	2.44	Uncued 50% [M-S]	-2.46	2.16	63	-0.70	-2.96	0.004	-0.305	7.04E+00
	-3.16	2.44	Uncued 50% [M]	-2.38	2.86	63	-0.78	-3.68	0.000	-0.294	4.97E+01
	-3.16	2.44	Cued 100% [M-S]	-4.25	4.30	63	1.09	2.17	0.034	0.322	1.22E+00
	-3.16	2.44	Cued 50% [M-S]	-3.61	3.51	63	0.44	0.95	0.346	0.149	2.10E-01
	-3.16	2.44	Cued 50% [M]	-3.45	4.16	63	0.28	0.60	0.552	0.086	1.63E-01
Uncued 50% [M-S]	-2.46	2.16	Uncued 50% [M]	-2.38	2.86	63	-0.08	-0.33	0.741	-0.031	1.44E-01
	-2.46	2.16	Cued 100% [M-S]	-4.25	4.30	63	1.79	3.73	0.000	0.553	5.79E+01
	-2.46	2.16	Cued 50% [M-S]	-3.61	3.51	63	1.15	2.84	0.006	0.404	5.28E+00
	-2.46	2.16	Cued 50% [M]	-3.45	4.16	63	0.98	2.14	0.036	0.311	1.15E+00
Uncued 50% [M]	-2.38	2.86	Cued 100% [M-S]	-4.25	4.30	63	1.87	4.08	0.000	0.521	1.71E+02
	-2.38	2.86	Cued 50% [M-S]	-3.61	3.51	63	1.22	2.81	0.007	0.384	4.91E+00
	-2.38	2.86	Cued 50% [M]	-3.45	4.16	63	1.06	2.39	0.020	0.303	1.90E+00
Cued 100% [M-S]	-4.25	4.30	Cued 50% [M-S]	-3.61	3.51	63	-0.64	-1.91	0.061	-0.165	7.55E-01
	-4.25	4.30	Cued 50% [M]	-3.45	4.16	63	-0.80	-2.72	0.008	-0.190	3.96E+00
Cued 50% [M-S]	-3.61	3.51	Cued 50% [M]	-3.45	4.16	63	-0.16	-0.57	0.573	-0.042	1.60E-01

Note. Contrasts represent paired samples Student’s t-tests.

Table A2.12

LRP amplitude contrasts

Comparator 1	M_1	SD_1	Comparator 2	M_2	SD_2	*df*	M_{diff}	*t*	*p*	*d*	BF_{10}
Uncued 100% [M-S]	-1.45	2.51	Uncued 50% [M-S]	-1.51	2.12	63	0.06	0.14	0.890	0.024	1.38E-01
	-1.45	2.51	Uncued 50% [M]	-1.53	2.11	63	0.08	0.21	0.838	0.035	1.40E-01
	-1.45	2.51	Cued 100% [M-S]	-1.45	2.55	63	0.00	-0.01	0.991	-0.001	1.37E-01
	-1.45	2.51	Cued 50% [M-S]	-1.71	2.00	63	0.26	0.67	0.505	0.116	1.70E-01
	-1.45	2.51	Cued 50% [M]	-1.37	2.07	63	-0.08	-0.20	0.843	-0.034	1.40E-01
Uncued 50% [M-S]	-1.51	2.12	Uncued 50% [M]	-1.53	2.11	63	0.03	0.13	0.899	0.012	1.38E-01
	-1.51	2.12	Cued 100% [M-S]	-1.45	2.55	63	-0.06	-0.14	0.888	-0.025	1.38E-01
	-1.51	2.12	Cued 50% [M-S]	-1.71	2.00	63	0.21	0.81	0.419	0.100	1.88E-01
	-1.51	2.12	Cued 50% [M]	-1.37	2.07	63	-0.13	-0.47	0.640	-0.063	1.52E-01
Uncued 50% [M]	-1.53	2.11	Cued 100% [M-S]	-1.45	2.55	63	-0.08	-0.22	0.829	-0.036	1.40E-01
	-1.53	2.11	Cued 50% [M-S]	-1.71	2.00	63	0.18	0.65	0.517	0.088	1.68E-01
	-1.53	2.11	Cued 50% [M]	-1.37	2.07	63	-0.16	-0.53	0.597	-0.075	1.57E-01
Cued 100% [M-S]	-1.45	2.55	Cued 50% [M-S]	-1.71	2.00	63	0.26	0.60	0.552	0.116	1.63E-01
	-1.45	2.55	Cued 50% [M]	-1.37	2.07	63	-0.07	-0.17	0.864	-0.032	1.39E-01
Cued 50% [M-S]	-1.71	2.00	Cued 50% [M]	-1.37	2.07	63	-0.34	-1.42	0.160	-0.166	3.57E-01

Note. Contrasts represent paired samples Student’s t-tests.

Table A2.13

LEP amplitude contrasts

Comparator 1	M_1	SD_1	Comparator 2	M_2	SD_2	*df*	M_{diff}	*t*	*p*	*d*	BF_{10}
Uncued 100% [M-S]	0.89	1.51	Uncued 50% [M-S]	0.90	1.34	63	-0.01	-0.05	0.961	-0.009	1.37E-01
	0.89	1.51	Uncued 50% [M]	1.01	1.43	63	-0.12	-0.43	0.670	-0.083	1.50E-01
	0.89	1.51	Cued 100% [M-S]	1.91	1.81	63	-1.02	-3.72	0.000	-0.614	5.70E+01
	0.89	1.51	Cued 50% [M-S]	1.37	2.29	63	-0.48	-1.47	0.146	-0.252	3.82E-01
	0.89	1.51	Cued 50% [M]	1.65	1.78	63	-0.76	-2.77	0.007	-0.460	4.49E+00
Uncued 50% [M-S]	0.90	1.34	Uncued 50% [M]	1.01	1.43	63	-0.11	-0.64	0.526	-0.078	1.66E-01
	0.90	1.34	Cued 100% [M-S]	1.91	1.81	63	-1.00	-4.07	0.000	-0.639	1.63E+02
	0.90	1.34	Cued 50% [M-S]	1.37	2.29	63	-0.46	-1.31	0.194	-0.256	3.10E-01
	0.90	1.34	Cued 50% [M]	1.65	1.78	63	-0.74	-2.49	0.016	-0.477	2.34E+00
Uncued 50% [M]	1.01	1.43	Cued 100% [M-S]	1.91	1.81	63	-0.90	-3.20	0.002	-0.553	1.34E+01
	1.01	1.43	Cued 50% [M-S]	1.37	2.29	63	-0.36	-1.13	0.264	-0.191	2.50E-01
	1.01	1.43	Cued 50% [M]	1.65	1.78	63	-0.64	-2.29	0.025	-0.395	1.54E+00
Cued 100% [M-S]	1.91	1.81	Cued 50% [M-S]	1.37	2.29	63	0.54	1.17	0.245	0.264	2.64E-01
	1.91	1.81	Cued 50% [M]	1.65	1.78	63	0.26	0.65	0.518	0.145	1.68E-01
Cued 50% [M-S]	1.37	2.29	Cued 50% [M]	1.65	1.78	63	-0.28	-1.23	0.224	-0.137	2.81E-01

Note. Contrasts represent paired samples Student’s t-tests.

Table A2.14

LPP amplitude contrasts

Comparator 1	M_1	SD_1	Comparator 2	M_2	SD_2	*df*	M_{diff}	*t*	*p*	*d*	BF_{10}
Uncued 100% [M-S]	-0.06	1.66	Uncued 50% [M-S]	-0.44	2.38	63	0.38	0.98	0.330	0.187	2.17E-01
	-0.06	1.66	Uncued 50% [M]	-0.49	2.75	63	0.42	1.00	0.323	0.193	2.20E-01
	-0.06	1.66	Cued 100% [M-S]	1.23	3.93	63	-1.30	-2.76	0.007	-0.464	4.39E+00
	-0.06	1.66	Cued 50% [M-S]	0.14	2.86	63	-0.21	-0.52	0.605	-0.092	1.56E-01
	-0.06	1.66	Cued 50% [M]	0.56	2.99	63	-0.63	-1.72	0.091	-0.268	5.47E-01
Uncued 50% [M-S]	-0.44	2.38	Uncued 50% [M]	-0.49	2.75	63	0.05	0.19	0.849	0.018	1.39E-01
	-0.44	2.38	Cued 100% [M-S]	1.23	3.93	63	-1.67	-2.86	0.006	-0.530	5.59E+00
	-0.44	2.38	Cued 50% [M-S]	0.14	2.86	63	-0.59	-1.49	0.141	-0.223	3.92E-01
	-0.44	2.38	Cued 50% [M]	0.56	2.99	63	-1.00	-1.99	0.050	-0.373	8.75E-01
Uncued 50% [M]	-0.49	2.75	Cued 100% [M-S]	1.23	3.93	63	-1.72	-2.73	0.008	-0.515	4.10E+00
	-0.49	2.75	Cued 50% [M-S]	0.14	2.86	63	-0.63	-1.40	0.166	-0.226	3.47E-01
	-0.49	2.75	Cued 50% [M]	0.56	2.99	63	-1.05	-1.90	0.062	-0.366	7.42E-01
Cued 100% [M-S]	1.23	3.93	Cued 50% [M-S]	0.14	2.86	63	1.09	1.58	0.119	0.320	4.44E-01
	1.23	3.93	Cued 50% [M]	0.56	2.99	63	0.67	1.07	0.287	0.194	2.37E-01
Cued 50% [M-S]	0.14	2.86	Cued 50% [M]	0.56	2.99	63	-0.42	-1.37	0.175	-0.142	3.34E-01

Note. Contrasts represent paired samples Student's t-tests.

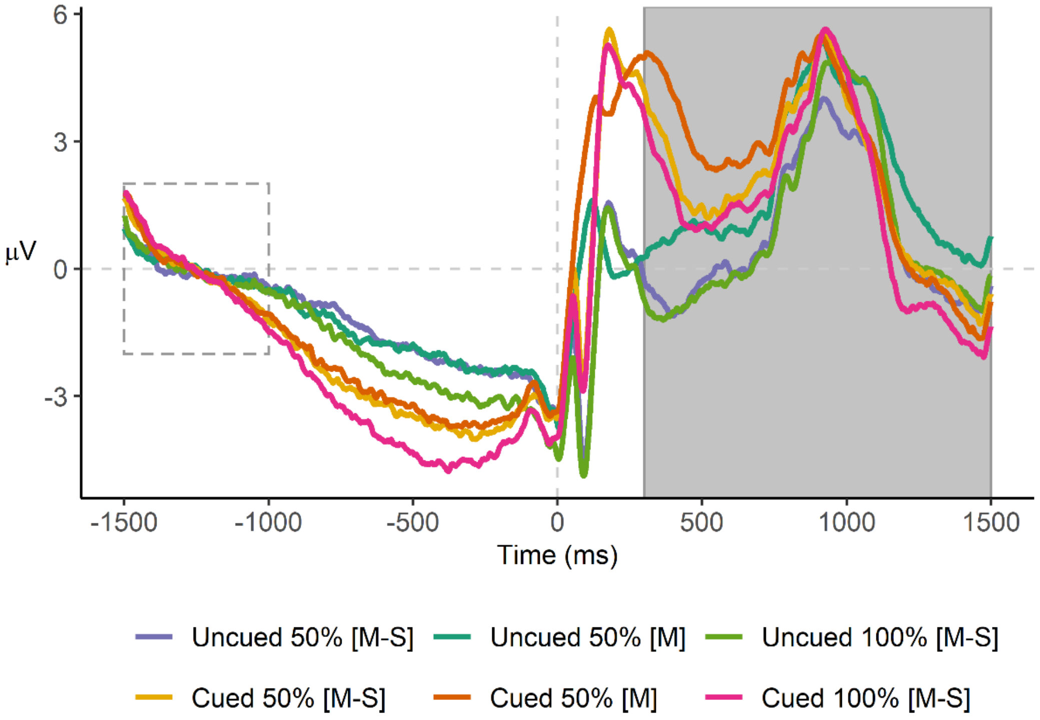
Table A2.15

Motor-corrected N1 amplitude contrasts

Comparator 1	M_1	SD_1	Comparator 2	M_2	SD_2	*df*	M_{diff}	*t*	*p*	*d*	BF_{10}
Uncued 100%	-4.11	2.39	Uncued 50%	-4.11	2.05	63	0.00	0.01	0.996	0.001	1.37E-01
	-4.11	2.39	Cued 100%	-3.54	2.44	63	-0.57	-2.08	0.042	-0.235	1.02E+00
	-4.11	2.39	Cued 50%	-3.47	2.32	63	-0.64	-1.82	0.073	-0.271	6.49E-01
Uncued 50%	-4.11	2.05	Cued 100%	-3.54	2.44	63	-0.57	-1.62	0.110	-0.253	4.70E-01
	-4.11	2.05	Cued 50%	-3.47	2.32	63	-0.64	-2.73	0.008	-0.294	4.02E+00
Cued 100%	-3.54	2.44	Cued 50%	-3.47	2.32	63	-0.07	-0.21	0.833	-0.031	1.40E-01

Note. Contrasts represent paired samples Student’s t-tests.

Fig. A2.1. Uncued and cued motor-stimulus block full epochs



Note. Shading indicates portion of epochs that may have been captured in the baseline correction period of subsequent trails (i.e., -1500 ms to -1000 ms, with a minimum ITI of 1800 ms).

Appendix 3

Table A3.1

Descriptive Statistics by Analysis Condition

		N1		P2		N2b	
Sequence	Task	*M*	*SD*	*M*	*SD*	*M*	*SD*
One-tone	Uncued Self-gen.	-3.95	3.94	1.11	3.05	0.64	3.48
	Cued Self-gen.	-3.98	3.66	0.93	3.53	0.17	4.25
	Uncued Listening	-4.80	3.41	2.76	3.07	2.04	3.10
	Cued Listening	-3.82	3.37	0.39	2.90	0.74	2.77
Two-tone	Uncued Self-gen.	-4.60	3.81	0.11	3.36	-1.10	4.03
	Cued Self-gen.	-4.65	4.25	1.21	4.53	-0.14	4.73
	Uncued Listening	-5.34	3.19	2.46	2.73	2.44	3.87
	Cued Listening	-4.51	3.51	1.96	2.50	0.72	3.09

Table A3.2

ANOVA Analysis of Component Amplitudes

		df_{num}	df_{den}	SS_{num}	SS_{den}	F	p	η_p^2	BF_{10}
N1	Intercept	0.98	58.85	9,682.97	4,359.78	133.26	<.001	0.69	1.00
	Sequence	0.86	51.72	49.24	249.14	11.86	.001	0.17	9.18
	Task	2.94	176.56	62.69	1,291.94	2.91	.036	0.05	1.76
	Sequence x Task	2.59	155.17	0.43	620.21	0.04	.989	0.00	0.02
P2	Intercept	0.74	44.38	1,263.58	1,722.12	44.02	<.001	0.42	1.00
	Sequence	0.77	45.95	15.09	542.04	1.67	.201	0.03	0.23
	Task	2.22	133.15	316.11	2,051.31	9.25	<.001	0.13	334,906.58
	Sequence x Task	2.30	137.84	25.46	774.34	1.97	.120	0.03	0.07
N2b	Intercept	0.82	49.11	231.76	2,488.19	5.59	0.021	0.09	1.00
	Sequence	0.80	47.73	21.04	589.62	2.14	0.149	0.03	0.26
	Task	2.46	147.33	453.50	2,547.14	10.68	0.000	0.15	4,336,194.87
	Sequence x Task	2.39	143.18	79.37	1,010.71	4.71	0.003	0.07	0.42

Table A3.3

Planned contrasts and interactions

				95% *CI*						
		Est.	*SE*	Lower	Upper	*df*	*t*	*p*	*d*	BF_{10}
N1	Volition	0.06	0.09	-0.11	0.23	180	0.72	.472	0.11	0.19
	Self-gen.	0.11	0.12	-0.13	0.35	180	0.90	.369	0.12	0.25
	Temp. Predict	0.49	0.21	0.08	0.90	180	2.34	.020	0.30	33.62
	Volition x Sequence	-0.00	0.10	-0.20	0.19	240	-0.05	.964	-0.01	0.16
	Self-gen. x Sequence	-0.02	0.14	-0.29	0.26	240	-0.13	.896	-0.02	0.17
	Temp. Predict x Sequence	-0.08	0.24	-0.55	0.40	240	-0.32	.751	-0.04	0.11
P2	Volition	-0.22	0.11	-0.44	-0.01	180	-2.09	.038	-0.31	1,223.77
	Self-gen.	-0.54	0.15	-0.84	-0.24	180	-3.57	<.001	-0.46	1,142.17
	Temp. Predict	-0.21	0.26	-0.72	0.31	180	-0.78	.435	-0.10	0.58
	Volition x Sequence	-0.22	0.12	-0.46	0.02	240	-1.78	.077	-0.27	0.40
	Self-gen. x Sequence	0.21	0.17	-0.13	0.55	240	1.21	.229	0.16	0.26
	Temp. Predict x Sequence	-0.05	0.30	-0.63	0.54	240	-0.16	.874	-0.02	0.19
N2b	Volition	-0.09	0.12	-0.32	0.15	180	-0.72	0.475	-0.11	51.43
	Self-gen.	-0.41	0.17	-0.74	-0.08	180	-2.41	0.017	-0.31	1,254.35
	Temp. Predict	-0.65	0.29	-1.22	-0.08	180	-2.23	0.027	-0.29	6,692.37
	Volition x Sequence	-0.44	0.13	-0.71	-0.18	240	-3.28	0.001	-0.49	3.57
	Self-gen. x Sequence	-0.17	0.19	-0.54	0.20	240	-0.88	0.379	-0.11	0.21
	Temp. Predict x Sequence	-0.21	0.33	-0.86	0.44	240	-0.63	0.528	-0.08	0.24

Table A3.4

ITI and Trial Count by Experimental Condition

Auditory Stimuli	Event Activation	Visual Stim.	ITI *M*	ITI *SD*	ITI *Min.*	Trial Count *M*	Trial Count *SD*	Trial Count *Min.*
Motor/Visual	Self-gen.	Cued	2,933.40	375.15	2,128.74	68.49	2.00	60
	Self-gen.	Uncued	2,916.04	356.39	2,120.75	66.89	3.49	50
	External	Cued	2,897.88	346.76	2,131.30	67.08	5.26	38
	External	Uncued	2,942.91	310.82	2,163.67	67.02	4.56	40
One-tone	Self-gen.	Cued	2,910.41	313.36	2,120.76	68.05	3.38	49
	Self-gen.	Uncued	2,922.47	340.13	2,139.94	67.34	3.70	50
	External	Cued	2,944.58	308.71	2,120.75	67.61	3.89	49
	External	Uncued	2,947.29	342.59	2,120.78	67.64	4.57	40
Two-tone	Self-gen.	Cued	2,955.33	354.33	2,125.44	68.39	2.44	57
	Self-gen.	Uncued	2,988.76	324.24	2,280.41	67.66	4.96	39
	External	Cued	2,934.07	323.45	2,126.85	68.16	3.25	48
	External	Uncued	2,918.98	315.04	2,174.28	67.74	3.85	48

Table A3.5

ANOVA Analysis of Inter-trial Intervals

	df_{num}	df_{den}	SS_{num}	SS_{den}	F	P	η_p^2	BF_{10}
Intercept	0.99	59.69	6.30E+09	6.29E+07	6,016.38	<.001	0.99	1.00
Auditory Stimuli	1.96	117.60	5.17E+03	4.28E+06	0.07	.930	0.00	0.02
Event Activation	0.84	50.70	1.35E+04	2.28E+06	0.35	.554	0.01	0.10
Visual Stimuli	0.94	56.39	8.13E+04	2.70E+06	1.81	.184	0.03	0.32
Auditory Stimuli x Event Activation	1.99	119.37	1.05E+04	2.93E+06	0.21	.807	0.00	0.04
Auditory Stimuli x Visual Stimuli	1.96	117.60	1.01E+03	2.64E+06	0.02	.977	0.00	0.03
Event Activation x Visual Stimuli	0.84	50.70	3.46E+04	1.02E+06	2.03	.159	0.03	0.21
Auditory Stimuli x Event Activation x Visual Stimuli	1.88	112.79	4.49E+04	3.57E+06	0.75	.472	0.01	0.11

Appendix 4

Table A4.1

Descriptive Statistics by Analysis Condition

		N1		P50	
ITI Split	Task	*M*	*SD*	*M*	*SD*
Short	Cued	-2.02	2.54	0.85	2.06
	Uncued	-3.98	2.21	-0.14	1.51
	Passive	-2.65	2.11	0.11	1.86
Long	Cued	-2.09	2.40	0.75	1.83
	Uncued	-2.53	2.67	-0.37	2.15
	Passive	-3.59	2.79	0.10	1.65

Table A4.2

ITI and Trial Count by Experimental Condition

			ITI			Trial Count		
ITI Split	Stimulus Gen.	Visual Stim.	*M*	*SD*	*Min.*	*M*	*SD*	*Min.*
Short	Motor-Stimulus	Inf.	2,011.38	268.58	1,707.70	41.03	5.77	14.00
	Motor-Stimulus	Uni.	2,015.74	267.54	1,716.65	39.95	6.93	13.00
	Motor	Inf.	2,007.56	270.79	1,704.48	41.42	5.15	14.00
	Motor	Uni.	2,086.84	366.85	1,589.73	39.53	7.07	14.00
	Visual-Stimulus	Inf.	2,015.69	271.30	1,716.61	41.34	4.91	14.00
	Visual	Inf.	2,018.09	269.48	1,716.58	41.45	4.93	14.00
Long	Motor-Stimulus	Inf.	2,815.66	504.12	1,877.47	41.79	5.73	15.00
	Motor-Stimulus	Uni.	2,809.88	499.65	1,882.87	40.68	7.00	13.00
	Motor	Inf.	2,815.84	498.06	1,888.91	42.13	5.09	15.00
	Motor	Uni.	2,854.03	578.72	1,970.90	40.18	7.14	15.00
	Visual-Stimulus	Inf.	2,815.53	505.91	1,878.20	42.21	5.07	14.00
	Visual	Inf.	2,811.55	502.42	1,885.35	42.05	4.95	15.00

Note. “Inf.” = informative, “Uni.” = uninformative.

Table A4.3

ANOVA Analysis of Inter-trial Intervals

	df_{num}	df_{den}	SS_{num}	SS_{den}	F	p	η_p^2
Intercept	0.51	19.02	1.33E+09	3.06E+07	1,610.33	<.001	0.98
Task	1.01	37.49	3.24E+04	8.79E+05	1.37	0.262	0.04
Auditory Stimuli	0.51	19.02	2.11E+04	3.94E+05	1.98	0.168	0.05
Task x Auditory Stimuli	1.01	37.49	4.61E+04	8.38E+05	2.03	0.138	0.05

Table A4.5

ANOVA Analysis of Component Amplitudes

		df_{num}	df_{den}	SS_{num}	SS_{den}	F	p	η_p^2
P50	Intercept	0.96	35.42	10.56	145.62	2.68	0.110	0.07
	ITI	0.99	36.62	0.71	89.39	0.30	0.590	0.01
	Task	1.91	70.85	43.65	270.76	5.97	0.004	0.14
	ITI x Task	1.98	73.24	0.47	279.58	0.06	0.939	0.00
N1	Intercept	0.98	36.09	1,797.49	469.30	141.72	<.001	0.79
	ITI	0.95	35.14	1.21	165.31	0.27	0.605	0.01
	Task	1.95	72.18	65.51	412.76	5.87	0.004	0.14
	ITI x Task	1.90	70.29	55.58	338.86	6.07	0.004	0.14

Table A4.6

Planned contrasts and interactions

		Est.	*SE*	95% *CI* Lower	95% *CI* Upper	*df*	*t*	*p*	*d*
P50	Self-generation	0.08	0.12	-0.16	0.33	74	0.66	0.508	0.15
	Volition	-0.50	0.21	-0.92	-0.07	74	-2.31	0.023	-0.44
	ITI	-0.11	0.24	-0.58	0.36	111	-0.46	0.644	-0.09
	Self-generation x ITI	-0.05	0.17	-0.39	0.28	111	-0.31	0.755	-0.06
	Volition x ITI	-0.06	0.30	0.52	-0.64	111	0.21	0.834	0.05
N1	Self-generation	-0.12	0.15	-0.41	0.18	74	-0.78	0.440	-0.18
	Volition	-0.98	0.26	-1.49	-0.47	74	-3.80	<.001	-0.72
	ITI	0.15	0.28	-0.41	0.70	111	0.52	0.606	0.10
	Self-generation x ITI	0.54	0.20	0.15	0.93	111	2.71	0.008	0.52
	Volition x ITI	0.76	0.35	1.44	0.09	111	2.21	0.029	0.51

Table A4.7

Descriptive Statistics by Counting Task Variant

		N1		P50	
ITI Split	Task	*M*	*SD*	*M*	*SD*
Short	Cued (Count)	-2.01	2.02	1.16	1.82
	Passive (Count)	-2.75	2.13	0.25	1.97
Long	Cued (Count)	-2.25	2.23	0.82	1.78
	Passive (Count)	-3.45	2.66	0.39	2.15

Table A4.8

ITI and Trial Count by Experimental Condition Counting Variants

			ITI			Trial Count		
ITI Split	Stimulus Gen.	Visual Stim.	*M*	*SD*	*Min.*	*M*	*SD*	*Min.*
Short	Motor-Stimulus (Count)	Cued	2,006.84	252.90	1,709.86	40.71	5.68	14.00
	Visual-Stimulus (Count)	Cued	2,017.57	269.44	1,716.62	41.21	5.33	13.00
Long	Motor-Stimulus (Count)	Cued	2,817.36	478.52	1,887.39	41.29	5.84	14.00
	Visual-Stimulus (Count)	Cued	2,814.77	504.56	1,878.59	41.87	5.48	13.00