Title:

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

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Abstract

Action-effect predictions are believed to facilitate movement based on its association with sensory objectives and suppress the neurophysiological response to self- versus externally-generated stimuli (i.e., sensory attenuation). However, research is needed to explore theorised differences in the use of action-effect prediction based on whether movement is uncued (i.e., volitional) or in response to external cues (i.e., stimulus-driven). While much of the sensory attenuation literature has examined effects involving the auditory N1, evidence is also conflicted regarding this component's sensitivity to action-effect prediction. 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 replicate recent evidence demonstrating reduced N1 amplitude for tones produced by stimulus-driven movement. Despite influencing motor preparation, action-effect contingency was not found to affect N1 amplitudes. Instead, we explore electrophysiological markers suggesting that attentional mechanisms may suppress the neurophysiological response to sound produced by stimulus-driven movement. Our findings demonstrate lateralised parieto-occipital activity that coincides with the auditory N1, corresponds to a reduction in its amplitude, and is topographically consistent with documented effects of attentional suppression. These results provide new insights into sensorimotor coordination and potential mechanisms underlying sensory attenuation.

Keywords:

Action-effect Contingency; Event-related Potential; Motor Preparation; Sensory Attenuation; Volition.

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., Schafer and Marcus 1973; Blakemore et al. 1998). This phenomenon has been attributed to the activity of internal forward models (IFMs; Miall and Wolpert 1996), in which duplicates of motor commands (i.e. 'efference copies'; von Holst and 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 and 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 (Prinz 1990; Prinz 1997; Hommel et al. 2001), 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.

While sensory attenuation has commonly been attributed to motor-based predictions within the IFM, evidence is conflicted regarding the influence of action-effect associations on the sensory response to self-generated stimuli. Although some data suggest that identity prediction (i.e., the ability to predict the precise nature of a stimulus, including tone frequency in the case of sound) may be associated with a reduced neurophysiological response to self-generated stimuli (Baess et al. 2008; Darriba et al. 2021), other investigations have not found this to be the case (Bednark et al. 2015; Dogge, Hofman, et al. 2019; Harrison et al. 2022). Several studies have even provided evidence of an enhanced response to predictable self-generated stimuli, including with respect to neurophysiological activity (Reznik et al. 2014; Yon et al. 2018; Reznik et al. 2021) and perceptual sensitivity (Reznik *et al.* 2014; Reznik et al. 2015; Dogge, Custers, Gayet, et al. 2019; Guo and Song 2019; Yon et al. 2021; Thomas et al. 2022). These discrepant findings have given rise to alternative accounts of sensory attenuation that have posited effects involving attentional differences (Horváth 2015), for example, and sensorimotor gating (Press et al. 2023).

From its origins in the ideomotor literature, the IFM was conceived to account for the influence of action-effect associations that are tightly coupled with bodily movements (e.g., tactile sensation from self-touch; Dogge, Custers and Aarts 2019; see Pfister 2019). Dogge, Custers and Aarts (2019) highlight an important distinction between these sorts of predictions (i.e., body-related) and those established based on interactions with one's surrounds (i.e., environment-related; e.g., auditory stimuli resulting from contact with an external object). Despite a wealth of research demonstrating effects of environment-related prediction on the processing of self-generated stimuli, Dogge, Custers and Aarts (2019) argue that evidence linking such effects to the IFM remains limited. Further research is therefore needed to clarify the influence of action-effect prediction based on environmental associations and explore mechanisms that may account for the observed phenomena.

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., in response to external stimuli) or volitional (i.e., enacted on the basis of its intended sensory effects; Herwig et al. 2007). Volitional movement has been distinguished from stimulus-driven action based on the degree of control that an agent has over *what*, *when* and/or *whether* motor activity is produced (Brass and Haggard 2008). While action-effect associations may be acquired based on either form of movement (see review by Pfister 2019), they are believed to play a more central role in the *production* of volitional action (Herwig *et al.* 2007; Pfister et al. 2011). In contrast, stimulus-driven movement may be initiated as a form of 'prepared reflex' in response to activating events and is therefore less reliant on action-effect associations (Hommel 2000). The distinction between these forms of action is also supported by research that has demonstrated recruitment of differing neuroanatomical structures (Krieghoff et al. 2011; Fried et al. 2017).

In addition to mechanistic distinctions between volitional movement and stimulus-driven action in terms of their production, recent findings have highlighted differences in the processing of resultant stimuli. Harrison et al. (2021) demonstrated a reduced primary cortical response to sounds resulting from stimulus-driven action compared with those arising from volitional movement. In comparison with the response elicited by externally-generated stimuli, only those arising from stimulus-driven movement were found to be suppressed. The mechanism underlying relative suppression of sensations resulting from stimulus-driven movement may therefore have relevance to understanding the sensory attenuation phenomenon. Overall, these findings highlight the need for further research comparing

stimulus-driven and volitional movement, including the role of action-effect prediction in both motor preparation and stimulus processing.

In this investigation, we aimed to delineate the influence of action-effect contingency on motor preparation for stimulus-driven and volitional movement, as well as the processing of resultant stimuli. To this end, we compared 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. Pre-stimulus analyses focused on the readiness potential and lateralised readiness potential (RP and LRP), as electrophysiological indices of motor preparation (see *ERP Components*). It was hypothesised that increased action-effect contingency would be associated with larger RP amplitudes, and that this effect would be greater for volitional movement compared with stimulus-driven action. Post-stimulus analyses focused on the auditory N1, as an index of neurophysiological activity in the primary auditory cortex and common subject of investigations into sensory attenuation (e.g., Schafer and Marcus 1973; Whitford et al. 2011; Schröger et al. 2015; Mifsud and Whitford 2017; Whitford et al. 2017; Jack et al. 2019; Han et al. 2021; Jack et al. 2021; Han et al. 2022). In accordance with Harrison *et al.* (2021), it was hypothesised that N1 amplitudes for sound produced by stimulus-driven action would be smaller than for those generated by volitional movement. We hypothesised that this effect may be associated with increased sensitivity of sensations resulting from stimulus-driven movement to differences in stimulus predictability. That is, it was anticipated that increased action-effect contingency would be associated with a reduction in N1 amplitudes and that this effect would be larger for stimulus-driven action than volitional movement.

Materials and Methods

Participants

The final sample included 64 healthy participants (45 female, 18 male and 1 other), aged between 17 and 36 years ($M = 20.09$, $Mdn = 19.16$, $SD = 3.01$). 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). Participants volunteered in exchange for course credit towards an undergraduate psychology unit at the University of New South Wales (UNSW). The study was approved by the UNSW Human Research Ethics Advisory Panel (Psychology) and written informed consent was obtained from participants prior to their involvement.

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°).
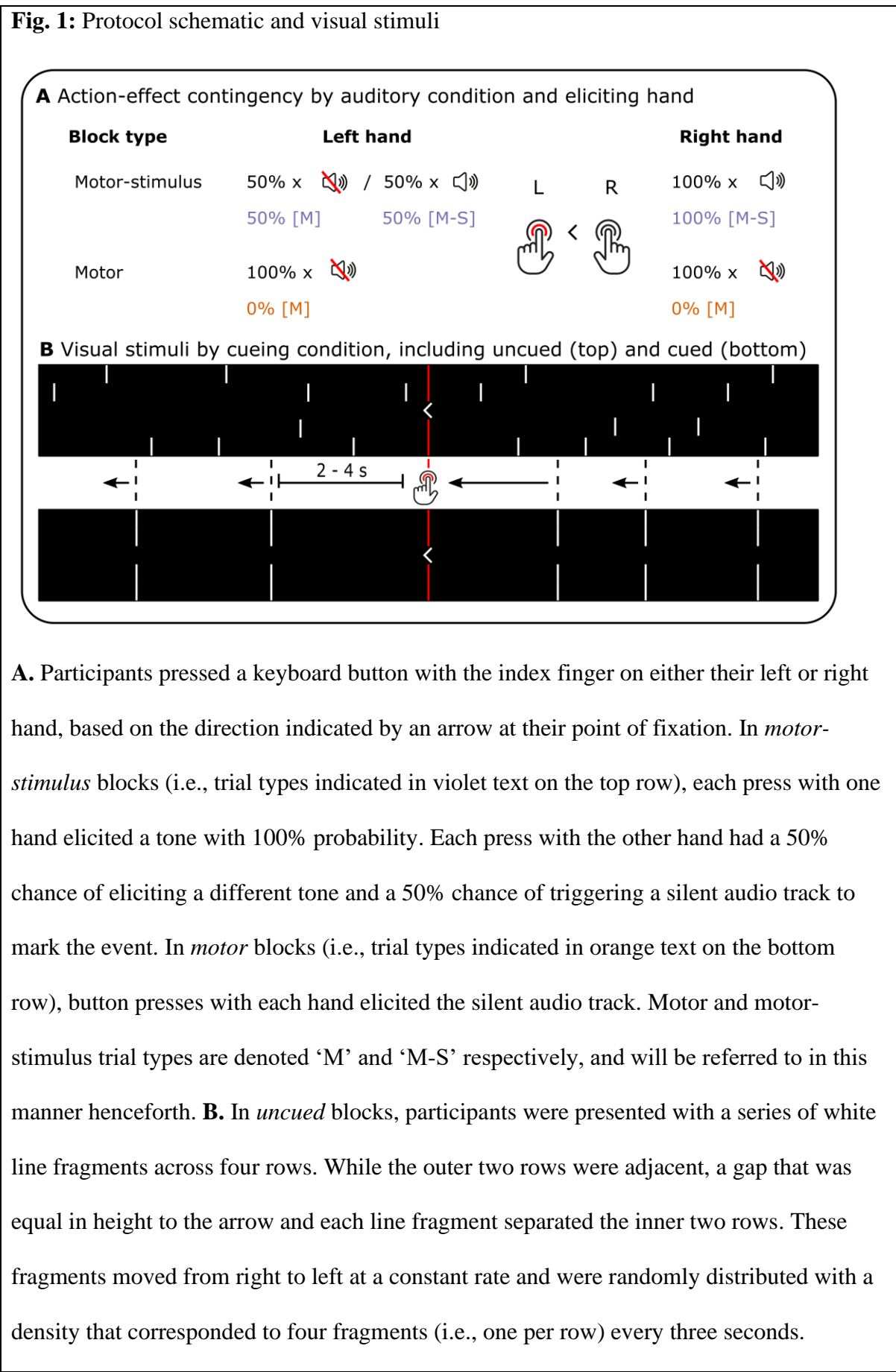
In two *uncued* block types (i.e., *motor-stimulus* and *motor*), a sequence of white line fragments appeared on the right side of the computer screen and moved leftward at a pace of approximately 3°/s (see Fig. 1B). The line fragments were of equal length and dispersed across four rows, spanning the 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. Movement in this condition was uncued in the sense that participants had agency with respect to when action was undertaken. 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. 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. 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.

EEG Processing

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. This ITI threshold was implemented to reduce differences in baseline correction associated with activity from the preceding trial, while maximising the number of trials retained for analysis. As participants were asked to leave a minimum of two seconds between button presses, this specific threshold was selected to

provide a small buffer for trials with short intervals. 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 S1 (see Supplementary Material).

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., Wohlert 1993; Pinheiro et al. 2020), 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. 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 S2 (see Supplementary Material). 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 smaller 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 and 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-03. Similarly, the interaction between *cueing* and *contingency* was not found to be statistically significant, $F(1.25, 78.45) = 1.152$, $p = .299$, $\eta_p^2 = .018$, $BF_{10} = 2.00E-03$.

ERP Components

Readiness Potential

The RP is a slow negative component that builds over motor areas in the lead-up to self-initiated movement (Kornhuber and Deecke 1965) and is generally believed to represent the final stages of motor preparation (Shibasaki and 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 and 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 more than for stimulus-driven action.

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., Vercillo *et al.* 2018; Wen *et al.* 2018; Pinheiro *et al.* 2020). In particular, the early RP

component is believed to involve bilateral activation of the Supplementary Motor Area (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 and Phillips 2009).

Lateralized Readiness Potentials

Unilateral hand movement is preceded by relative negativity over the contralateral hemisphere (Deecke et al. 1976). This activity, known as the LRP, can also be observed in moments following presentation of a cueing stimulus (Kutas and 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 and Miller 1995), though not its forcefulness (Sommer et al. 1994). Unlike the centralised RP, action-effect contingency was not found by Reznik *et al.* (2018) and Vercillo *et al.* (2018) to influence LRP amplitudes. However, Hughes and Waszak (2011) showed that LRP amplitude was increased for voluntary actions eliciting a visual outcome, compared to actions not associated with any sensory consequences. Several prior studies have also yielded evidence that, when self-paced, LRP amplitudes do not differ on the basis of whether movement is cued or selected by participants (i.e., forced versus free choice between left- and right-hand movement, for example; Waszak et al. 2005; Keller et al. 2006; Kiesel et al. 2006). In an experiment requiring speeded responses to stimuli occasionally interrupting voluntary actions, Hughes et al. (2011) demonstrated that increased lateralised motor activity

related to voluntary action selection is associated with faster stimulus-driven responding, suggesting that the LRP indexes movement preparation independent of the domain of action selection (voluntary versus stimulus-driven). In addition to control over the timing of action, conditions in this experiment differed on the basis of action selection (i.e., both *when* and *how* to move). To our knowledge, the LRP has not previously been examined in research that has isolated effects associated with action timing (i.e., movement that differs with respect to volitional control over *when* it is enacted).

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 did not change for 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 and Gaspelin 2017). This was taken as the most negative local minimum between -200 and 0, which was found to have occurred at -70 ms.

Lateralized Enactment and Post-enactment Potentials

During investigation of the LRP, two additional distinct maxima were observed within the collapsed localiser waveform (see Fig. 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. 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.

Auditory N1

The N1 is a large negative component that is commonly studied in sensory attenuation research (e.g., Lange 2011; Whitford *et al.* 2017; Klaffehn et al. 2019). 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 (Näätänen and Picton 1987; Giard et al. 1994). One subcomponent, described as the N1b (McCallum and 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 elicited by 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.

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 (Näätänen and Picton 1987; Woods 1995; Whitford *et al.* 2017; Harrison *et al.* 2021). 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 and 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.

Statistical Analyses

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). Orthogonal contrasts were used to investigate effects across levels of the *contingency* variable and their interaction with *cueing*. In accordance with the procedure described by Field et al. (2012), these were assessed based on equivalent linear regressions with random intercepts that varied by participant among the *contingency* and *cueing* factors. Levels of the *contingency* factor were compared based on two orthogonal contrasts, which supported comparison of the 100% and 50% probability conditions, as well as the motor and motor-stimulus variants of the 50% conditions (see Table 1). These contrasts will be described henceforth as the effects of *probability* and *action-effect*. Bayes Factors were also produced for the effects contained within the ANOVAs, based on Cauchy priors with an r-scale of $1/\sqrt{2}$ (Morey and 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 1

Orthogonal contingency contrasts

Condition	Contrast	
	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.

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 $1/\sqrt{2}$.

Results

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 Tables A1 and A2, respectively (see Appendix). Results of the ANOVAs and contrasts are reported in full in Tables S3 and S4, respectively (see Supplementary Material).

Readiness Potential

The ANOVAs revealed a significant main effect of *cueing* in both the early RP, $F(0.89, 56.06) = 31.34$, $p < .001$, $\eta_p^2 = 0.332$, $BF_{10} = 2.12E+15$, and late RP, $F(0.94, 59.38) = 7.47$, $p = .008$, $\eta_p^2 = 0.106$, $BF_{10} = 5.01E+03$ (see Fig. 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, $t(126) = 1.84$, $p = .069$, $d = 0.327$, $BF_{10} = 1.75E+00$, 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, $t(126) = 2.17$, $p = .032$, $d = 0.386$, $BF_{10} = 7.82E-01$. 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. 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, $t(126) = 2.27$, $p = .025$, $d = 0.405$, $BF_{10} = 3.53\text{E}{+}00$, with larger amplitude observed in the higher probability condition (i.e., 100%) compared with the lower probability conditions (i.e., 50%).

Lateralized Readiness Potential

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

**Fig. 2:** Readiness and lateralised readiness potential analyses
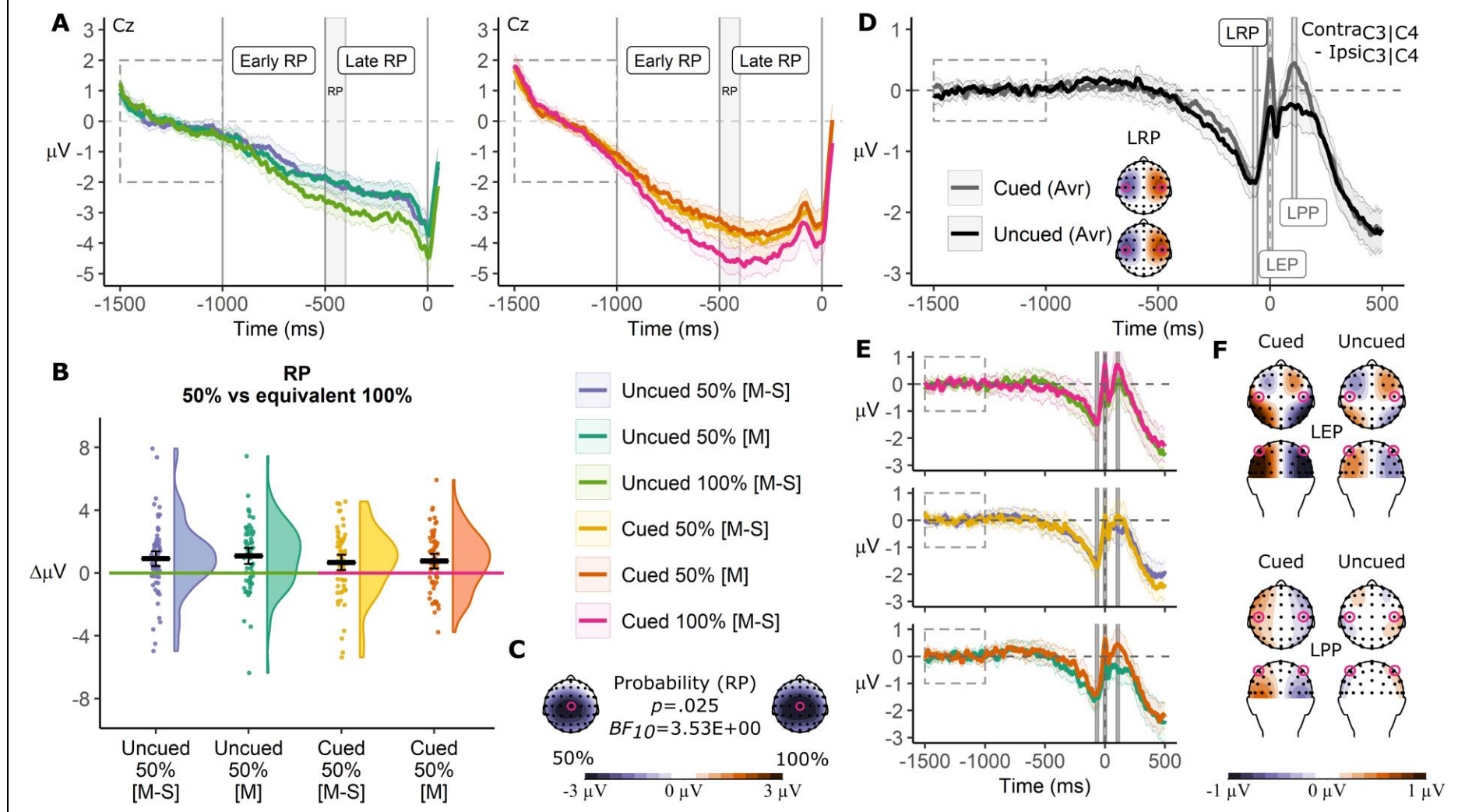
A. Grand-averaged recordings at Cz, demonstrating mean amplitude and 95% CI by uncued condition (left) and cued condition (right). **B.** Within-subject differences in late RP amplitude between 50% and equivalent 100% conditions (i.e., cued or uncued), with mean differences and 95% CIs. **C.** Topographic 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.

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. 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. 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*. The ANOVA results indicated a significant effect of *cueing* on LEP amplitude, $F(0.73, 46.29) = 24.60$, $p < .001$, $\eta_p^2 = 0.281$, $BF_{10} = 3.96\mathrm{E}{+}02$, such that the LEP was larger (i.e., more positive) for *cued* conditions. In contrast, effects were non-significant with respect to *contingency,* $F(1.43, 89.80) = 0.80$, $p = .450$, $\eta_p^2 = 0.013$, $BF_{10} = 6.09\mathrm{E}{-}02$, and the *cueing* x *contingency* interaction*,* $F(1.47, 92.59) = 0.74$, $p = .479$, $\eta_p^2 = 0.012$, $BF_{10} = 1.14\mathrm{E}{-}01$. 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, η_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, η_p^2 = 0.036, *BF$_{10}$* = 2.87E-01, and the *cueing* x *contingency* interaction, *F*(1.44, 90.54) = 0.64, *p* = .528, η_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) = 0.10, *p* = .923, *d* = 0.014, *BF$_{10}$* = 1.28E-01.

Fig. 3: Lateralised enactment and post-enactment potential analyses
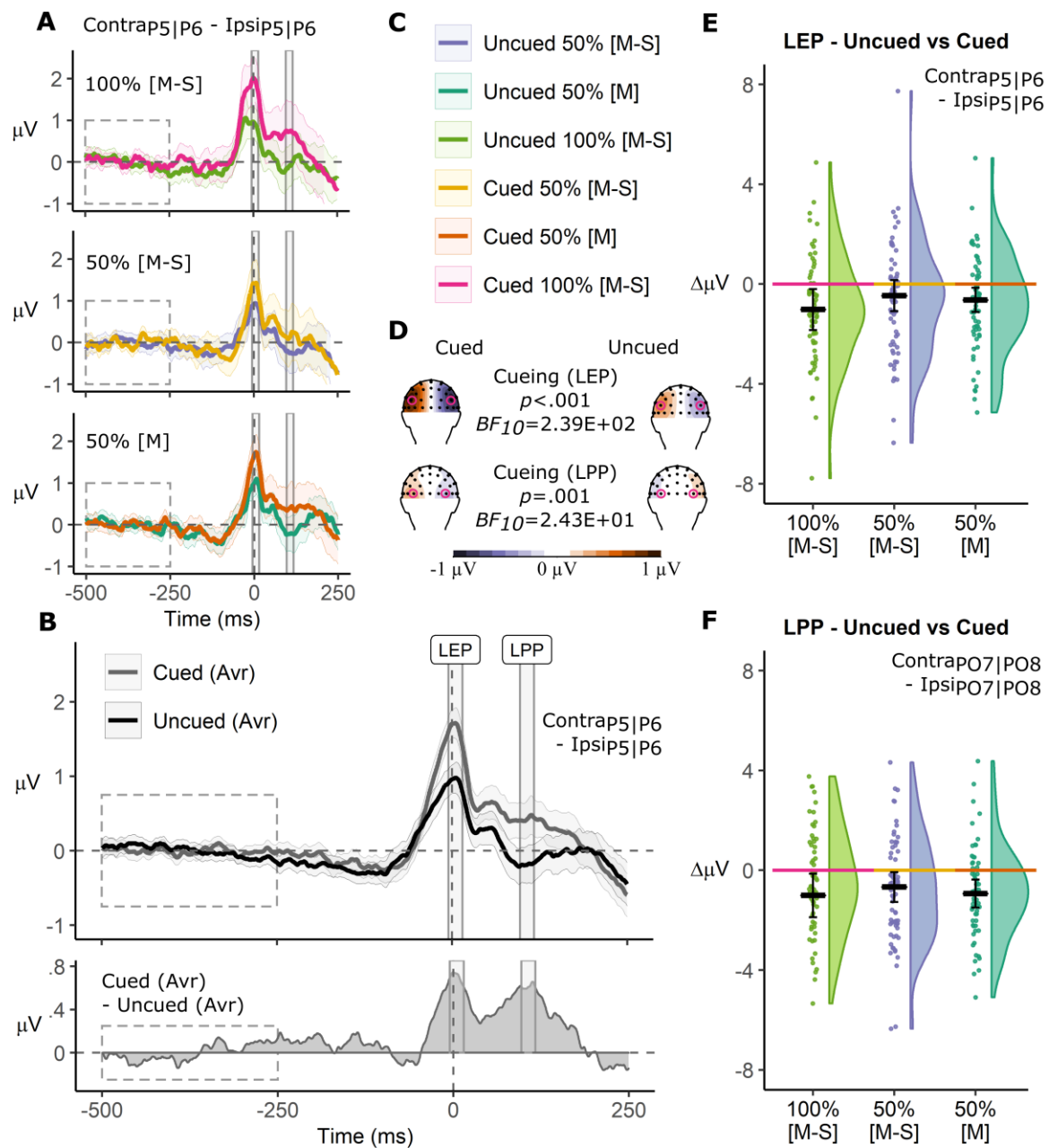
A. Difference in grand-averaged voltage recordings at P5 and P6 (i.e., contralateral minus ipsilateral) for cued and uncued variants by probability condition, including 100% [M-S] (top), 50% [M-S] (middle) and 50% [M] (bottom). **B.** Difference in grand-averaged voltage recordings at P5 and P6 (i.e., 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.

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.

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 A3 (see Appendix), while results

of the ANOVA are reported in Table S5 (see Supplementary Material). The ANOVA

revealed a statistically significant main effect for *cueing*, $F(1, 63) = 9.67$, $p = .003$, $\eta_p^2 =$

$.133$, $BF_{10} = 4.27E+00$ (see Fig. 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. 4: Motor-corrected N1 analyses
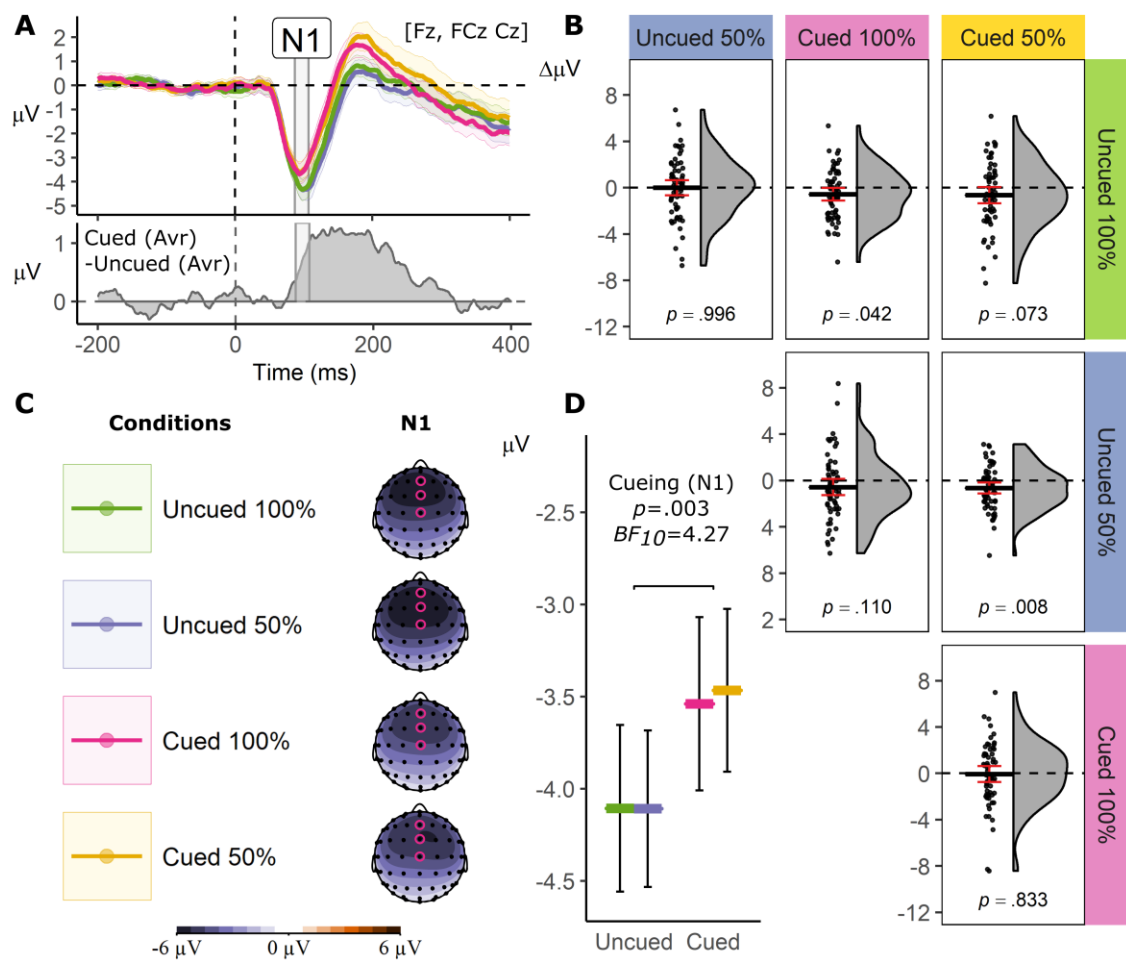
A. Motor-corrected auditory evoked potentials (top), representing pooled mean amplitudes at Fz, FCz and Cz by condition, as well as 95% CIs. Difference between collapsed cued and uncued conditions (bottom), demonstrating sustained attenuation of cued conditions between approximately 100 ms and 200 ms 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.

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). These analyses were undertaken using G*Power (Faul et al. 2007). At $α = .05$ (two-tailed), the sample was found to be sufficient to detect small ($η_p^2 = .01$), medium ($η_p^2 = .06$) and large ($η_p^2 = .14$) two-level repeated measures main effects with powers of .354, .978, and >.999, respectively.

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 occurred 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. S1 in *Supplementary Material*). 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 characteristics. 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 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.

Although 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 and 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.

Results from the present investigation contribute to recent findings that have drawn into question the role of motor-based predictions in sensory attenuation (see review by Press *et al.* 2023). Action-effect contingency was not found to affect N1 amplitude, and the associated Bayes Factor indicated substantial evidence in favour of a null effect. These results are therefore consistent with other studies demonstrating that N1 amplitudes may not be influenced by motor-based prediction (Bednark *et al.* 2015; Dogge, Hofman*, et al.* 2019; Harrison *et al.* 2022). As much of the sensory attenuation literature has explored effects relating to the N1 (e.g., Curio et al. 2000; Ford et al. 2001; Houde et al. 2002; Heinks-Maldonado et al. 2005; Ford et al. 2007; Jack *et al.* 2021), these findings may have wide-ranging theoretical implications and highlight the need to further distinguish the effects of suppression from mechanisms underlying such phenomena (see Press et al. 2022).

In conjunction with Harrison *et al.* (2021), our findings may support the notion that attentional factors contribute to the phenomenon of sensory attenuation (e.g., Horváth et al. 2012; Horváth 2015). Harrison *et al.* (2021) found that N1 amplitudes to tones resulting from volitional action do not differ from those of externally-generated tones when these are made predictable in time. Because differences in temporal predictability have been identified as a common methodological confound in sensory attenuation research (see Hughes et al. 2013), its effects may account for the suppression of stimuli resulting from volitional movement in other investigations (Schafer and Marcus 1973; Baess *et al.* 2008; Sato 2008; Baess et al. 2011; Jack *et al.* 2021). In contrast, and in accordance with the present results, Harrison *et al.* (2021) observed reduced N1 amplitudes for tones resulting from stimulus-driven movement. As our results appear to implicate attentional factors in the suppression of N1 amplitudes to stimulus-driven movement, they may also suggest that sensory attenuation is driven to some degree by such influences.

While we found that tones resulting from stimulus-driven movement were associated with relative positivity that spanned the N1 and P2 latencies, self-generated stimuli have been associated with suppressed (i.e., more *negative*) P2 amplitudes relative to those produced externally (e.g., Bolt and Loehr 2021; Harrison *et al.* 2021; Jack *et al.* 2021; Bolt and Loehr 2023). These findings are in accordance with Harrison *et al.* (2021), who found suppressed P2 amplitudes in response to tones elicited by volitional movement compared to those that resulted from stimulus-driven action or were externally-generated. As the observed pattern of suppression cannot account for sensory attenuation of the P2 component, further research is needed to explore associated mechanisms. Previous research has argued that P2 amplitudes are reduced when stimuli are subject to higher levels of attentional control, including processes involved in its termination (see García-Larrea et al. 1992; Crowley and Colrain 2004). One possibility may therefore be that the absence of attentional suppression during volitional movement necessitates increased attentional control to disengage from resulting stimuli.

Our findings may serve to highlight the importance of distinguishing between environment- and body-related predictions. As argued by Dogge, Custers and Aarts (2019), evidence of IFM-based sensory attenuation is stronger with respect to body-related predictions than with those involving environment-related associations. Results from the present investigation provide further indication that this framework may not account for the suppression of self-generated stimuli generated by one's interactions with their surrounds. Relatedly, Press *et al.* (2023) highlight that the attenuation of self-generated stimuli may involve quasi-predictive mechanisms associated with sensorimotor gating (e.g., tactile sensations associated with movement of an effector limb). To the extent that such mechanisms rely on phylogenetically-established associations, as posited by Press *et al.* (2023), this may account for the distinct effects of environment- and body-related prediction.

There were several limitations to the present study that warrant acknowledgement. Firstly, volitional movement and stimulus-driven action were distinguished on the basis of whether the timing of participants' movement was cued or uncued. As discussed by Brass and Haggard (2008), this represents just one dimension of agency. While volitional movement was 'uncued' in the sense that participants could select *when* to act, visual cues indicated *what* action was to be undertaken in both the volitional and stimulus-driven conditions. Similarly, the conditions did not differ with respect to participants' agency over *whether* to move. That is, both conditions may be considered volitional in the sense that participants had agency over whether to follow instructions. Further research is needed to explore effects associated with these other dimensions of volitional control. Nevertheless, the present findings demonstrate clear sensorimotor differences based on whether movement is initiated according to one's own timing or that of external cues.

Secondly, while we have tentatively attributed the LEP and LPP to effects involving motor-based attentional suppression and postulate a relationship with sensory attenuation, we cannot rule out alternative explanations. For example, relative suppression of N1 amplitudes to tones resulting from stimulus-driven movement may reflect heightened demand for visual attention or cognitive control rather than the suppression of attention to auditory stimuli per se. In a similar experiment by Harrison *et al.* (2021), N1 amplitudes to tones produced by stimulus-driven movement were not found to be sensitive to the manipulation of attention towards visual cues. However, future research may explore potential differences in the influence of such effects on stimulus-driven and volitional movement.

Thirdly, several caveats are warranted with respect to conclusions about the influence of action-effect contingency. In relation to those associated with RP amplitude, findings may be limited by the differing frequency of trials for each condition. That is, to complete equal numbers of action-effect trials based on probabilities of 50% and 100%, participants pressed

twice as frequently with the finger that produced these 50% of the time. Present findings

cannot rule out the possibility that larger RP amplitudes in the 100% condition reflect

increased motor preparation for less frequently produced movement. It is worth noting,

however, that Reznik *et al.* (2018) demonstrated similar RP effects based on a design

comparing motor and motor-stimulus conditions (i.e., 0% and 100% contingencies) that were

produced with equal frequency in mixed blocks. More generally, the comparison of 50% and

100% contingency may not represent a contrast that is strong enough to elicit meaningful

differences in the neurophysiological response. Future investigations may serve to address

this limitation by reducing the probability of an action-effect on each given trial or randomly

perturbing the identity of stimuli (e.g., the pitch of tones) in the low-contingency condition.

This may be particularly relevant to research comparing sensorimotor processing associated

with stimulus-driven and volitional movement.

Finally, it is important to acknowledge limitations with respect to the precise aspect of

the neurophysiological response represented in these data. Although the supratemporal N1 is

commonly believed to reflect activity within the primary auditory cortex (Näätänen and

Picton 1987; Giard *et al.* 1994), Horváth (2015) highlights evidence suggesting that the

attenuation of this component may reflect effects across a more diffuse range of cortical

structures. Further investigation is therefore needed to delineate the anatomical substrates of

the observed effects and their relevance to the sensory attenuation phenomenon. This

research may be particularly important to reconcile our findings with research demonstrating

attenuation of self-generated stimuli in other aspects of the evoked response.

Conclusions

Findings from the present investigation indicate that, despite an apparent role in motor

preparation, action-effect contingency does not influence primary cortical response to

resultant stimuli. This is in contrast 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). 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 movement. 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. These findings may warrant a review of theoretical accounts of the sensory attenuation phenomenon. We propose that the effect of sensory attenuation may differ with respect to volitional and stimulus-driven action, and is at least partly supported by differences in selective attention.

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Author Contributions

A.W.H: Conceptualization, Methodology, Software, Formal Analysis, Investigation, Data Curation, Writing – Original Draft, Visualization, Project Administration. **G.H:** Conceptualization, Writing – Review & Editing. **G.R:** Conceptualization, Writing – Review & Editing. **B.K.C:** Conceptualization, Writing – Review & Editing. **T.J.W:** Conceptualization, Methodology, Software, Validation, Resources, Writing – Review & Editing, Supervision, Project Administration, Funding Acquisition.

Competing Interests

The authors have no competing interests to declare.

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Appendix

Table A1

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

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 A3

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