

RESEARCH ARTICLE

WILEY

Pre-movement event-related potentials and multivariate pattern of EEG encode action outcome prediction

Edward Ody  | Tilo Kircher | Benjamin Straube | Yifei He

Department of Psychiatry and Psychotherapy,
University of Marburg, Marburg, Germany

Correspondence

Edward Ody, Department of Psychiatry and
Psychotherapy, University of Marburg, Rudolf
Bultmann-Strasse 8, 35039 Marburg,
Germany.
Email: edward.ody@uni-marburg.de

Funding information

Deutsche Forschungsgemeinschaft,
Grant/Award Numbers: 286893149,
222641018; Hessisches Ministerium für
Wissenschaft und Kunst

Abstract

Self-initiated movements are accompanied by an efference copy, a motor command sent from motor regions to the sensory cortices, containing a prediction of the movement's sensory outcome. Previous studies have proposed pre-motor event-related potentials (ERPs), including the readiness potential (RP) and its lateralized sub-component (LRP), as potential neural markers of action feedback prediction. However, it is not known how specific these neural markers are for voluntary (active) movements as compared to involuntary (passive) movements, which produce much of the same sensory feedback (tactile, proprioceptive) but are not accompanied by an efference copy. The goal of the current study was to investigate how active and passive movements are distinguishable from premotor electroencephalography (EEG), and to examine if this change of neural activity differs when participants engage in tasks that differ in their expectation of sensory outcomes. Participants made active (self-initiated) or passive (finger moved by device) finger movements that led to either visual or auditory stimuli (100 ms delay), or to no immediate contingency effects (control). We investigated the time window before the movement onset by measuring pre-movement ERPs time-locked to the button press. For RP, we observed an interaction between task and movement. This was driven by movement differences in the visual and auditory but not the control conditions. LRP conversely only showed a main effect of movement. We then used multivariate pattern analysis to decode movements (active vs. passive). The results revealed ramping decoding for all tasks from around -800 ms onwards up to an accuracy of approximately 85% at the movement. Importantly, similar to RP, we observed lower decoding accuracies for the control condition than the visual and auditory conditions, but only shortly (from -200 ms) before the button press. We also decoded visual vs. auditory conditions. Here, task is decodable for both active and passive conditions, but the active condition showed increased decoding shortly before the button press. Taken together, our results provide robust evidence that pre-movement EEG activity may

Benjamin Straube and Yifei He contributed equally to this study.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2023 The Authors. *Human Brain Mapping* published by Wiley Periodicals LLC.

represent action-feedback prediction in which information about the subsequent sensory outcome is encoded.

KEYWORDS

action prediction, ERP, forward model, MVPA, readiness potential

1 | INTRODUCTION

The brain is constantly anticipating and preparing for future events. Voluntary actions are preceded by a planning period in which aspects of the movement, such as its goal, trajectory and timing are prepared (Haggard, 2008). Importantly, this motor planning is essential for the brain to anticipate the sensory consequences of actions, in order to distinguish between self- and externally generated sensations which are otherwise identical and therefore ambiguous to our sensory receptors (Bansal et al., 2018). According to theories of sensorimotor control, this predictive process is achieved through an efference copy-based forward model mechanism (Wolpert, 1997). The efference copy (von Holst & Mittelstaedt, 1950) is a copy of the motor command for a movement which is sent from the motor cortex to the appropriate sensory cortices prior to and during the execution of an action, containing a prediction for its outcome. Neural and behavioural responses to correctly predicted sensations are subsequently modulated (Arikan et al., 2019; Baess et al., 2011; Fuehrer et al., 2022; Lubinus et al., 2022; Martikainen et al., 2005; Ody et al., 2023; Press et al., 2020; Reznik et al., 2021; Sanmiguel et al., 2013; Straube et al., 2017; Weiss et al., 2011; Yon et al., 2018), allowing us to identify those sensations as our own (e.g., during speaking) and retain a sense of agency and consciousness (e.g. Blakemore & Frith, 2003).

While a great deal of studies have shown modulated perception of an action's sensory outcome, motor control theories have been also attested by studies that examine neural activity preceding action execution. To date, this line of study primarily focuses on pre-motor cortical potentials, recorded with electroencephalography (EEG), within which the efference copy of a voluntary action, e.g., whether the action leads to a stimulus or not (contingency), or whether the action induces visual, auditory, or tactile feedback (modality), may be encoded. The efference copy may be represented in the 'readiness potential' (RP; Kornhuber & Deecke, 2016), a slow negative event-related potential (ERP), typically with a fronto-central scalp distribution, that occurs 1–2 s prior to the execution of a voluntary movement. The RP is usually split into early (beginning between 1.5 and 2 s before movement) and late (beginning around 400–500 ms before movement) phases (Brunia et al., 2012). The early phase of the RP is thought to be related to activation in the supplementary motor area (SMA), as the largest amplitude is seen along the midline (Brunia et al., 2012; Deecke, 1987). The late phase shows a steeper change in amplitude and greater lateralisation than the early phase. It has therefore been connected to activation of the primary motor cortex (M1; Brunia et al., 2012; Deecke, 1987). There is evidence that both the

efference copy and the RP may originate in the SMA. Haggard and Whitford (2004) had participants judge the amplitudes of motor-evoked potentials (MEPs) produced with TMS, either with or without concurrent voluntary actions. MEPs were judged to be smaller when an action was performed, demonstrating sensory suppression. However, when TMS was used over the SMA, shortly before the movement onset, the suppression effect was almost completely abolished. This suggests that the efference copy is generated in the SMA, and that sensory suppression does not occur without it. Evidence from intracranial recordings (Fried et al., 2011; Ikeda et al., 1992; Rektor et al., 1994) and dipole source analysis (Praagstra et al., 1996) indicate the involvement of the SMA in generating the RP.

Several studies have shown that the RP encodes upcoming action feedback (Jo et al., 2014; Pinheiro, Schwartz, Gutiérrez-Domínguez, & Kotz, 2020; Reznik et al., 2018; Vercillo et al., 2018; Wen et al., 2018). Reznik et al. (2018) found that RP was more negative preceding button presses that triggered a tone compared to button presses that triggered no stimulus. RPs preceding externally generated tones did not however show a significant change in amplitude from baseline. This suggests that the RP contains a unique predictive component related to motor prediction for the sensory consequences of the action, that cannot be explained by mere expectation of an auditory event. Vercillo et al. (2018) employed a similar design with visual feedback and found that the late RP was more negative before actions with effects compared to no effects. Pinheiro, Schwartz, Amorim, et al. (2020); Pinheiro, Schwartz, Gutiérrez-Domínguez, and Kotz (2020) found that the late phase of the RP for actions with sensory feedback predicted N1 suppression in healthy participants, non-clinical voice hearers and psychotic patients with auditory verbal hallucinations. Pinheiro, Schwartz, Amorim, et al. (2020); Pinheiro, Schwartz, Gutiérrez-Domínguez, and Kotz (2020) found similarly modulated RP for both real and imagined sounds compared to button presses with no feedback. RP is also related to the reliability of the action consequence (Wen et al., 2018) and to intentional binding (Jo et al., 2014).

While these studies unanimously show that RP is related to the action consequence, the results regarding the early and late phases of the RP are not consistent. For example, Jo et al. (2014) found that the early (but not the late) phase was related to action-feedback processing. Vercillo et al. (2018) found that late phase RPs were more negative before actions with effects, whereas the early phase showed the opposite pattern. Wen et al. (2018) found that both phases of the RP had increased amplitudes preceding actions with consistent compared to inconsistent effects. Pinheiro, Schwartz, Amorim, et al. (2020); Pinheiro, Schwartz, Gutiérrez-Domínguez, and Kotz (2020) found

that real and imagined sensory consequences were associated with larger early and late phase RP amplitudes but found only the early phase was sensitive to the stimulus type (self-voice vs. tone). Therefore, evidence for a functional dissociation of early and late phases of the RP in encoding sensory consequences is inconclusive.

A few studies have also reported that the lateralized RP (LRP; Gratton et al., 1988) may differ as a function of an action's contingency. The LRP is seen before unilateral movements, as a negativity over the hemisphere contralateral to the chosen effector. This lateralization typically begins close to the execution of the action but can also occur well before the movement if the participant is instructed with which hand to use (Kutas & Donchin, 1980). The component is believed to represent motor-specific and lower-level motor preparatory activity, originating in the primary motor cortex (M1) (Brunia et al., 2012). Accordingly, studies that have reported RP sensitivity to action-effect contingency observed no effects of LRP (Reznik et al., 2018; Vercillo et al., 2018). However, notably, Hughes and Waszak (2011) found larger LRP (and not RP) amplitudes for button presses that triggered a visual stimulus compared to when the button presses that triggered no stimulus. Ford et al. (2014) found that participants with larger LRPs preceding their button press showed greater differences between N1 for self-generated and externally generated tones. Thus, unlike the RP, whether the LRP represents merely motor-specific specifications of the action, or whether it also entails prediction of the action's contingency remains controversial.

So far, the literature seems to unanimously suggest that, before the execution of a voluntary action, the motor-sensory system starts to prepare for the upcoming stimulus. However, it is not known how prediction is implemented in the case of involuntary movements. Specifically, when someone performs an action, but involuntarily (e.g., being moved by a device), does the pre-movement neural activity reflect the prediction of the action's sensory outcome? It is claimed that RP is specific for voluntary actions (Shibasaki & Hallett, 2006). However, the absence of these potentials does not necessarily imply that the neural activity prior to involuntary action does not encode predictive information of the action, because a task-relevant action is nevertheless performed. Involuntary movements present an interesting case for studying motor planning because they allow for good control over temporal prediction for the upcoming stimulus, and over tactile and proprioceptive feedback. However, they presumably do not involve the same level of motor planning as voluntary movements, nor should they be accompanied by an efference copy.

In this study, we wanted to investigate how action-effect contingency may be represented in pre-movement neural activity for both voluntary and involuntary movements. We employed a device which uses an electromagnet to produce the involuntary movements (passive movement device). This and similar devices have been used in several previous studies (Arikan et al., 2017, 2019; Ody et al., 2023; Pazen et al., 2020; Schmitter et al., 2021; Schmitter & Straube, 2022; Straube et al., 2020; Uhlmann et al., 2020, 2021; van Kemenade et al., 2016). Participants made active (self-initiated) or passive (finger moved by device) movements. The movements were either followed

by a stimulus (visual or auditory, 100 ms delay) or by no immediate action effect (control). We examined whether the typical neural markers of motor planning (RP and LRP) encode the upcoming movement (active or passive) and task (visual, auditory or control).

To date, EEG studies on motor planning have exclusively focused on the RP and the LRP. However recently, this conventional univariate approach has been complemented by the emerging multivariate pattern analysis (MVPA) methods. MVPA refers to a set of techniques for analysing neuroimaging data. Unlike conventional univariate techniques, which typically compare single measures of activity (e.g., the amplitude in a set of voxels or electrodes under different conditions), MVPA takes the relationships between multiple variables into consideration and is thus more sensitive, specific, and flexible than its univariate counterparts (Grootswagers et al., 2017). MVPA was first applied to fMRI data (Haxby et al., 2001) but there has been a growing number of studies applying the technique to neural time series data (Carlson et al., 2013; J.-R. King et al., 2014; Li et al., 2022; Schaefer et al., 2011). A popular MVPA technique in EEG research is decoding across time (DAT), which involves training a machine learning algorithm to classify trials based on amplitudes of all (or multiple) electrodes as belonging to two or more different conditions. By carrying out this process across multiple time points (i.e. train on time point t_0 and test on time point t_0), the resulting time series of performance measures illustrates how two or more conditions can be differentiated over time. RP is known to have a wide topographic distribution (Shibasaki & Hallett, 2006) and large between-subject variance in polarity (Trovò et al., 2021). DAT elegantly handles this type of variance. Therefore, we performed DAT, complementary to RP, to investigate how movement preparation and action-effect contingency are represented across the whole scalp.

Taking the principle a step further, if a classifier is trained on each time point (t_0) and tested on every other time point (t_1), known as temporal generalisation (TG), the resulting classification matrix suggests the degree to which the underlying brain processes may overlap across different time windows (J. R. King & Dehaene, 2014). This technique enables us to query the dynamics of brain activity over time, and several patterns describing different processes (e.g., isolated stages, sustained, ramping, or oscillating activity) have been suggested (J. R. King & Dehaene, 2014). Given that TG provides the possibility to reveal the relationship between distinct processing stages in brain activity across time, we employed this technique to examine whether we could identify the putative early and late phases of the RP. Depending on the pattern revealed, we could infer whether pre-movement neural activity consists of an early and a late phase of processing.

We hypothesised that RPs would encode the upcoming movement type, with greater amplitudes for the active condition, as we expected motor preparation activity to differ between the active and passive movements. Additionally, we predicted larger differences between the movement types when the movements were followed by an action effect (visual, auditory) compared to no immediate effect (control), as we expected there to be additional predictive processes in the active condition, related to anticipating the upcoming self-

initiated action feedback. For the LRPs, the majority of previous research suggests that it does not encode action-effect contingency. The LRP has been related to low-level motor processes originating in M1. Therefore, while there may be a general anticipation for the upcoming passive movement, we did not expect motor-specific preparatory activity in this condition. Therefore, we hypothesised that LRPs would encode movement type but not task. For the DAT analysis, we hypothesised that decoding accuracy for distinguishing between active and passive movements would be higher for the visual and auditory conditions than the control condition, due to additional outcome prediction in the active condition of the former. Based on the evidence that RP comprises an early and a late phase, we expected these to be revealed in the TG analysis.

As participants completed both a visual and auditory task, another possibility to investigate how action-effect contingency is represented in pre-motor activity is to decode the task modality. We conducted a second set of MVPA analyses (DAT and TG) in which we trained the classifier to decode visual and auditory task modality, separately for the active and passive conditions. We expected that the pre-movement window would contain a prediction for the upcoming sensory consequences of the action and therefore hypothesised that the task modality would be decodable before the button press. We also expected that the decoding accuracy between the active and passive conditions in this analysis is different. Notably, prior literature that directly compares active vs. passive (self-initiated vs. externally induced) movements focuses predominantly on the sensory perception of the action-induced stimuli. Based on univariate ERP approaches, they showed mixed findings (BäB et al., 2008; Hughes & Waszak, 2011; Martikainen et al., 2005; Mifsud et al., 2016). Using MVPA, a few recent studies reported enhanced perception of stimuli induced by active movements (e.g., Yon et al., 2018, 2023), but no literature has directly used MVPA to examine motor-preparatory EEGs. Thus, due to a lack of directly comparable previous literature, we refrain from hypothesising the direction of this comparison.

2 | MATERIALS AND METHODS

2.1 | Participants

Twenty-nine participants (nineteen females) took part in the study. The age range was between 19 and 31 ($M = 23.7$, $SD = 3.35$). Participants were recruited through a university mailing list at the University of Marburg and received €30 for taking part. The study was approved by the local ethics committee in accordance with the Declaration of Helsinki (except for pre-registration World Medical Association, 2013). All participants provided written informed consent. Participants were right-handed, had normal or corrected-to-normal hearing and vision, no history of mental illness, no history of drug or alcohol abuse, no history of serious brain injury and no first-degree relatives with schizophrenia, as assessed by self-report. Participants were naïve to the purpose of the experiment. Due to a technical error with the

presentation software, one participant was missing data and therefore 28 participants were included in the analyses.

2.2 | Task and procedure

Different analyses from the same dataset have been reported in Ody et al. (2023). The procedure is therefore the same but is reported again in brief here. Participants sat in front of a 19" 60 Hz computer monitor in a semi-darkened room. The participant's right index finger was securely attached to a button mounted on a custom-built button box with a piece of elastic. Participants responded to the task with their left hand, using the computer keyboard. Then, 45 dB pink noise was played through headphones throughout the experiment to mask the sound of the button press. Before completing the main experimental blocks, participants completed a training exercise consisting of five blocks of five trials each. The EEG cap was then fitted.

Participants made active or passive button presses. Active button presses were self-initiated while passive button presses were produced by pulling the finger down with the passive movement device. After the button press, participants engaged in an intensity judgement task. They judged the intensity of either two grey discs (visual condition) or two tones (auditory condition), which were consecutively presented with an inter-stimulus interval between them. Alternatively, in a third condition (control condition), participants completed the visual task in 50% of trials and the auditory task in the other 50% of trials. However, the task stimuli were presented with a 1000 ms delay after the button press. The experiment, therefore, had a 2×3 repeated measures design with the factors of movement (active, passive) and task (visual, auditory, control). A schematic of the trial structure is presented in Figure 1 and histograms of the time durations between the cue onset (fixation cross enlargement) and the button press is displayed in Figure 2.

Each trial started with a black fixation cross. After a randomly chosen interval between 500 and 1500 ms (in 250 ms steps), the cross enlarged. This acted as a cue indicating that participants could press the button at their own pace (active conditions) or that the button would shortly move (passive conditions). In passive conditions, the button fired after a randomly chosen interval between 500 and 1250 ms (in 83 ms steps). In the visual and auditory task conditions, there was a fixed 100 ms interval before the first stimulus was shown. This short delay was included to ensure that the timing of the stimulus was always predictable, even in the passive condition when the button press timing could not be predicted. In the control condition, there was instead a 1000 ms interval before the stimulus was shown. There was then an inter-stimulus interval between 500 and 1250 ms (in 250 ms steps), followed by the second stimulus. The first stimulus was presented at a fixed intensity while the second could vary between 5 values. After another 500 ms interval, the question 'Welcher war heller?' or 'Welcher war lauter?' ('which was brighter/louder', in German) was displayed. Participants responded with the 'v' (first stimulus brighter/louder) and 'n' (second stimulus brighter/louder) keys to indicate their decision. Making a response triggered a

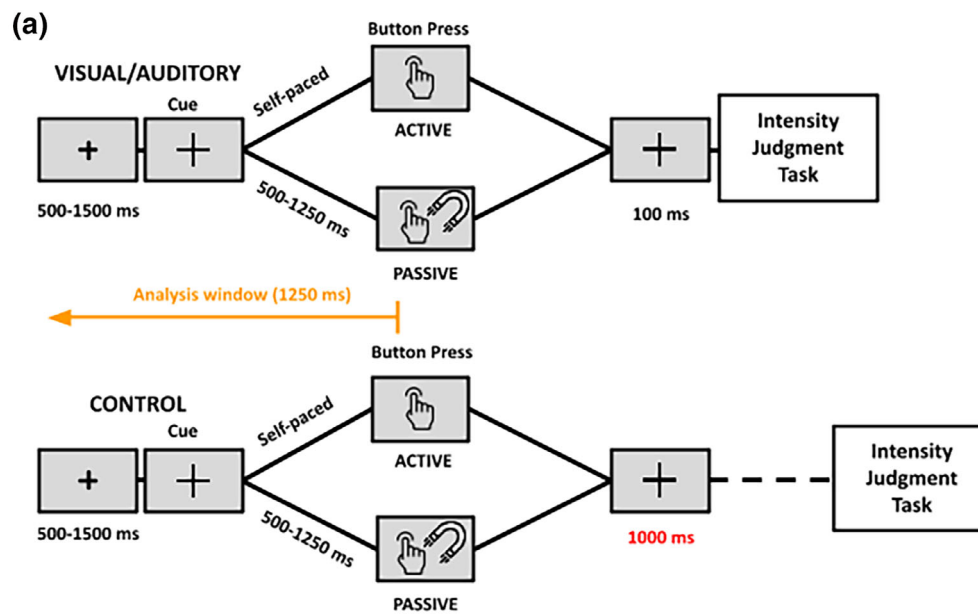


FIGURE 1 Schematic of the trial structure. (a) Schematic of the button press procedure in the visual/auditory and control conditions. The analysis window (time-locked to the active/passive button press) is indicated by the orange arrow. In the visual and auditory conditions, there was a 100 ms delay after the button press before the task was presented while the control condition had a 1000 ms delay before the task was presented. (b) The behavioural task. Participants were presented with two disks (visual) or tones (auditory) and judged the intensity difference between these stimuli (brighter or louder).

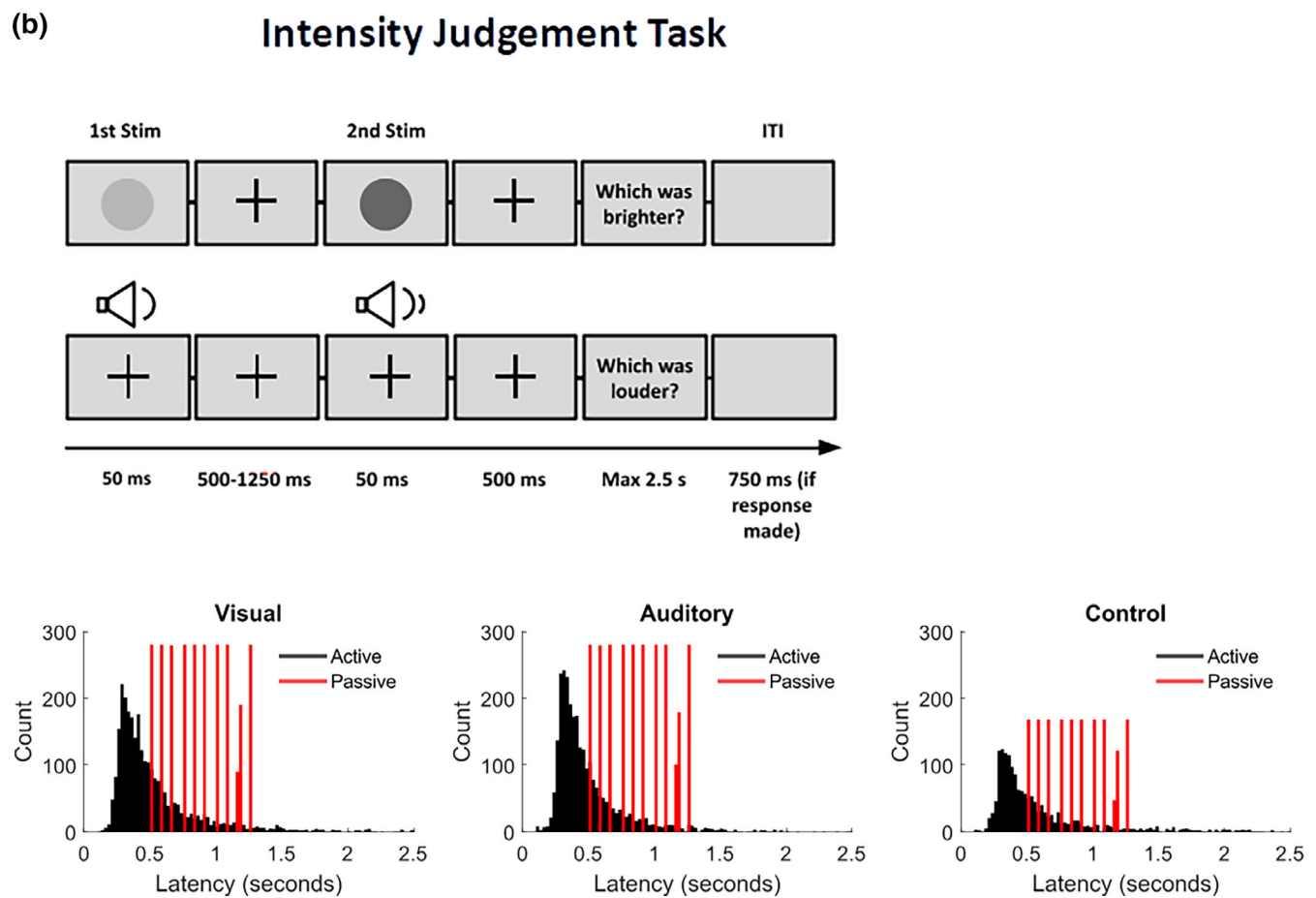


FIGURE 2 Histograms showing the distribution of time durations between the cue onset (fixation cross enlargement) and the button press across all participants and all trials.

750 ms inter-trial interval and if no response was made after 2.5 s, the next trial started automatically. In auditory trials, the fixation cross remained on screen during stimulus presentation and disappeared

when the question was presented. In visual trials, it disappeared while the stimuli were displayed but remained on-screen during the inter-stimulus interval and between the stimulus and question. In all

conditions, the fixation cross remained on screen during the interval between the button press and the first stimulus presentation. Comparison stimuli were presented in a pseudorandom order where the same stimulus level was not shown on more than two consecutive trials.

Visual, auditory, and control trials were presented in separate blocks. The visual and auditory blocks had 200 trials each (100 active and 100 passive) and the control block had 120 trials (60 active and 60 passive). Within the blocks, active and passive trials were presented as mini blocks of 25 (visual, auditory) or 15 (control) at a time, in an alternating fashion (e.g., 25 active, 25 passive etc.). In the control block, the first 60 trials had the visual task and the second 60 had the auditory task.

2.3 | Stimuli

Stimuli were presented with Psychtoolbox (V 3.0.12) running on Octave (V 4.0.0) in Linux. Auditory stimuli consisted of a 1000 Hz tone. The first tone was always presented at 74 dB, whereas the second had a loudness of 71, 72.5, 74, 75.5, or 77 dB. Visual stimuli consisted of a solid 250-pixel disc. The first disc was always presented at a luminance of 11.42 cd/m², whereas the second had a luminance of 8.84, 9.94, 11.42, 12.69, or 14.04 cd/m². Stimuli were presented for 50 ms. Luminance measurements were performed using an i1Display Pro photometer (X-Rite Pantone, Grand Rapids, USA). Volume measurements were performed using an RS-95 decibel metre (RS Components Ltd). The stimuli were presented on a fixed grey background with a luminance of 3.40 cd/m².

2.4 | EEG data acquisition

EEG was continuously recorded at a sampling rate of 500 Hz from 32 active Ag/AgCl electrodes (Fp1/2, F7/8, F3/4, Fz, FT9/10, FC5/6, FC1/2, T7/8, C3/4, Cz, TP9/10, CP5/6, CP1/2, P7/8, P3/4, Pz, O1/2, and Oz). The EEG was referenced online to the electrode location FCz and the ground electrode was placed on the forehead. Impedances were kept at 25 k Ω or below. The signal was amplified by a BrainVision amplifier and recorded with BrainVision Recorder (Brain Products GmbH, Germany). Electrodes were mounted in an elastic cap (actiCAP, Brain Products GmbH, Germany) according to the international 10–20 system.

2.5 | EEG preprocessing

Preprocessing was completed using the EEGLAB toolbox (Delorme & Makeig, 2004) in MATLAB (R2020a Mathworks, Sherborn, MA). EEG data were downsampled to 250 Hz and re-referenced to the average of electrodes TP9 and TP10. Line noise was removed using the Zapline Plus function (Klug & Kloosterman, 2022). A high-pass filter was applied at 1 Hz and the data were subjected to an extended

infomax ICA. Components were classified using ICLabel (Pion-Tonachini et al., 2019) and any that were identified as muscle, eye or channel noise with greater than 79% estimated accuracy were removed. The ICA results were then applied to the unfiltered data. Finally, the data were band-pass filtered between 0.01 and 100 Hz.

Further analyses were completed with the Fieldtrip toolbox and custom routines in MATLAB (R2020a Mathworks). Trials in which the participant failed to make a response to the behavioural task and trials with unusually short button press response times (less than 100 ms) were excluded from all subsequent analyses. EEG was segmented into epochs from 1.3 s before to 0.5 s after the button press. A band-pass filter was applied between 0.01 and 40 Hz. Channels which had a range greater than 300 μ V in more than 50% of trials were removed and interpolated using the ft_channelrepair function from the Fieldtrip toolbox (Oostenveld et al., 2011) with spline interpolation. This procedure resulted in two channels being interpolated (in different participants). Trials were then submitted to an additional artefact rejection routine. Those with a range greater than 300 μ V and/or with large variance (greater than 10 standard deviations above or below the mean z-transformed data) in any channel were removed. These steps were implemented with the ft_artifact_zvalue and ft_artifact_threshold functions from Fieldtrip. The data were baseline corrected to the period between 1 and 1.25 s before the button press.

At the end of preprocessing, the mean (standard deviation) percentage of trials removed across all participants was 16.26% (9.58%).

MVPA and permutation tests were implemented in MATLAB using the MVPA-Light (Treder, 2020) toolbox and permutest function (Gerber, 2023). Statistical analyses (repeated measures ANOVA, Bayesian statistics) were implemented in JASP (Love et al., 2019). For the Bayesian statistics, we followed the recommendations given by Keyzers et al. (2020). Accordingly, Bayesian ANOVAs were conducted with default priors, and effects are reported as the Bayes factor for the inclusion of a particular effect (BF_{inc}), calculated as the ratio between the likelihood of the data given the model with versus the next simpler model without that effect. Post hoc pairwise comparisons were conducted using Bayesian paired Samples *t* tests using default effect size priors (Cauchy scale 0.707). Results are reported using the two-tailed Bayes factor BF_{10} that represents $p(\text{data}|\text{H}+:\text{factor1} \neq \text{factor2}) / p(\text{data}|\text{H}0:\text{factor1} = \text{factor2})$. The magnitude of Bayes factors was interpreted according to (Andraszewicz et al., 2015) (i.e. anecdotal, moderate, strong, very strong, or extreme etc. evidence for the alternative/null hypothesis).

2.6 | Readiness potential and lateralized readiness potential

For RP analyses, data were averaged across electrodes Cz, C3, and C4. LRP was calculated by subtracting the average of electrode C3 from the average of electrode C4.

For statistical analysis, we did not have an a priori hypothesis regarding the exact time window(s) in which the conditions would differ. Therefore, we first tested the general difference between the

active and passive conditions (averaged across visual, auditory and control) using a cluster-based permutation test. All time points were first tested with two-tailed-dependent samples t tests with a significance level of $p < .05$. Contiguous time points exceeding this threshold were grouped into clusters and the sum of the t values was used as the test statistic for the permutation test. This process was repeated 1000 times (1000 permutations) with shuffled condition labels, to determine a distribution of the probability of observing a cluster (or clusters) with that test statistic value. Clusters within the highest or lowest 2.5th percentile were considered significant.

The permutation tests revealed significant time windows shortly before the button press for both RP and LRP (see Sections 3.1 and 3.2 for details). We then based our second analysis on these time windows. We calculated the mean amplitude across the significant time window (only including those before the button press, as we were interested in pre-movement activity only), resulting in one value per condition, per participant. We then subjected these values to a 2×3 repeated measures ANOVA with the factors of movement (active, passive) and task (visual, auditory, control). Where appropriate, Bonferroni-corrected post hoc pairwise comparisons were conducted. We also conducted repeated measures Bayesian ANOVAs. JASP does not support post hoc comparisons for interaction effects. Therefore, for the RP, where there was strong evidence for the interaction effect, we tested the comparisons of interest using paired-samples Bayesian t tests. See Section 3.1 for details.

2.7 | Multivariate pattern analysis- active versus passive movement

The EEG segments (preprocessed as described in Section 2.5) were downsampled to 50 Hz, in order to reduce processing time for these computationally intensive analyses. For DAT, we trained a linear discriminant analysis (LDA) classifier (McLachlan, 2005) to discriminate the movement type (active or passive) at each time point, using all channels as features. This was done separately for the three task conditions (visual, auditory, control). We used the default hyperparameter $\lambda = 0.1$ (magnitude of shrinkage regularisation; Ledoit & Wolf, 2004), with fivefold cross-validation, 100 repeats and 30 features (EEG channels). The accuracy of the classifier at each time point was used as the performance metric. The resulting time series was tested using a cluster-based permutation test (two-tailed dependent samples t test, p -value threshold = .05, 1000 permutations) at the group level, to identify clusters where the accuracy was significantly above chance (0.5). We then performed further cluster-based permutation tests to compare the decoding accuracies between the different task conditions. The tests had the same parameters, except that the test statistic underwent a Bonferroni correction for multiple comparisons (two comparisons per condition, $p = .05/2$).

For TG, the LDA was trained to discriminate active and passive movements at each time point and (t_0) and tested on every other time point (t_1), resulting in one two-dimensional matrix of classification accuracies for each task condition (visual, auditory, control). All

channels were included as features. The classification parameters in the TG analysis were set identically to the DAT analysis. Statistical significance was decided based on comparing the 2D matrices to a matrix of chance level performance (0.5) of identical dimensions, using a cluster-based permutation test (two-tailed dependent samples t test, p -value threshold = .05, 1000 permutations).

2.8 | MPVA—Visual versus auditory sensory modality

The method for testing visual versus auditory sensory modality was the same as described in Section 2.8, except for the following differences. First, the LDA classifiers were trained to discriminate sensory modality (visual or auditory). This was repeated separately for active and passive movements. The permutation test comparing the active and passive time series was only compared once and therefore did not need to undergo Bonferroni correction.

3 | RESULTS

3.1 | Readiness potential

The cluster-based permutation test comparing active and passive movements (across all task conditions) revealed a significant time window extending from ~ 200 to ~ 20 ms before the button press (Figure 2a). The ANOVA on mean amplitudes in this time window showed extreme evidence of a main effect of movement, $F(1, 27) = 16.16$, $p = <.001$, $\eta_p^2 = .37$, $BF_{\text{incl}} = 1376.4$, extreme evidence for a main effect of task, $F(2, 54) = 9.29$, $p = <.001$, $\eta_p^2 = .26$, $BF_{\text{incl}} = 602.4$, and extreme evidence of an interaction between movement and task, $F(2, 54) = 6.33$, $p = .003$, $\eta_p^2 = .19$, $BF_{\text{incl}} = 132.7$. To further investigate the interaction, we conducted post hoc comparisons. For the frequentist statistics, the reported p -values have been Bonferroni-corrected for multiple comparisons. In particular, we were interested in the movement differences within the three task conditions. For the visual task, there was strong evidence for the difference between active and passive ($t = 3.58$, $p = .009$, $BF_{10} = 17.5$) with higher amplitudes for active (mean = $0.45 \mu\text{V}$) than passive (mean = $-1.02 \mu\text{V}$). For the auditory task, there was extreme evidence for a difference between active and passive ($t = 4.55$, $p < .001$, $BF_{10} = 421$) with greater amplitudes for active (mean = $1.77 \mu\text{V}$) than passive (mean = $-0.1 \mu\text{V}$). In the control condition, there was moderate evidence for there being no effect of movement ($t = 0.38$, $p = 1$, $BF_{10} = 0.2$). All other comparisons are reported in the supplement (Table S1). RP results are presented in Figure 2.

3.2 | Lateralized readiness potential

LRPs for active versus passive movements across all tasks were significantly different within around -140 to 70 ms afterwards. For the

ANOVA, we only considered time points before the button press (−140 to 0 ms). Repeated-measures ANOVA revealed extreme evidence for a main effect of movement, $F(1, 27) = 19.28$, $p < .001$, $\eta_p^2 = .417$, $BF_{\text{incl}} = 118.3$. For the effect of task, $F(2, 54) = 0.5$, $p = .609$, $\eta_p^2 = .018$, $BF_{\text{incl}} = 0.08$, and the interaction between movement and task, $F(2, 54) = 0.15$, $p = .862$, $\eta_p^2 = .005$, $BF_{\text{incl}} = 0.05$, there was strong evidence in favour of the null hypothesis. LRP results are presented in Figure 4.

3.3 | MVPA—Active versus passive movement

In the DAT, all three task conditions showed significantly above chance (0.5) decoding accuracies for identifying the movement type (active vs. passive) from around 800 ms before the button press onwards. For the comparisons between conditions, there was a significant cluster showing higher decoding accuracy for visual compared to control beginning ~250 ms before the button press. There was a similar cluster showing higher decoding accuracy for auditory than control beginning ~230 ms until ~30 ms before the button press.

In the TG, the visual and auditory conditions showed slowly ramping generalisation from ~1 s before the button press. The control condition showed a similar ramping pattern which became significant later at approximately 750 ms before the button press. MVPA results for decoding movement (active vs. passive) are presented in Figure 5.

3.4 | MVPA—Visual versus auditory sensory modality

In the DAT, the active and passive conditions showed ramping decoding accuracy that was significantly above-chance decoding from around 400 ms before the button press onwards. Decoding accuracy was significantly higher in the active condition than the passive condition from approximately 150 ms before the button press onwards.

For TG, both conditions showed ramping decoding from around 1 s before the button press onwards.

MVPA results for decoding sensory modality (visual vs. auditory) are presented in Figure 6.

4 | DISCUSSION

In this study, we investigated electrophysiological activity preceding active and passive button presses which were associated with either visual or auditory stimuli (100 ms delay) or with no immediate effects. Passive movements were executed by the finger being pulled down with an electromagnet-powered device. We first examined two typical neural markers of motor preparation, the RP and LRP. We then conducted MVPA to determine how action-effect prediction was distributed across the whole scalp. Our MVPA and RP (but not LRP) results consistently show that pre-movement neural activity encodes

the action's contingency. These results emphasise the importance of pre-movement neural activity in the processing of self- and externally generated sensory consequences (Arikan et al., 2019; Baess et al., 2011; Fuehrer et al., 2022; Lubinus et al., 2022; Martikainen et al., 2005; Ody et al., 2023; Sanmiguel et al., 2013; Straube et al., 2017).

4.1 | The role of RP in action contingency

It has been argued that RP and LRP are specific for voluntary, active movements (Shibasaki & Hallett, 2006). However, empirical evidence is sparse, especially based on the comparison with involuntary movements. In this study, we looked at EEG activity preceding movements induced by a passive movement device for the first time. We observed robust differences between active and passive movements for both RP and LRP, from around ~200 ms on. These findings suggest that both of these neural markers reflect the difference between movements, be it physical, motoric, or predictive (Pinheiro, Schwartz, Amorim, et al., 2020; Pinheiro, Schwartz, Gutiérrez-Domínguez, & Kotz, 2020; Reznik et al., 2018; Vercillo et al., 2018).

The functional dissociation between the RP and the LRP is evident from the observed interaction between movement and task. Importantly, this interaction was significant for the RP but not the LRP. The interaction was driven by larger differences between the active and passive movements in the visual and auditory conditions than in the control condition. Here, in the control condition, the movement difference was not significant and the Bayes factor suggested moderate evidence that there was no difference. In other words, the movement differences were only present when there was an immediate action-effect contingency. This finding suggests that the RP does not merely reflect low-level processes, but is also sensitive to differences in high-level, predictive mechanisms that differ between active and passive movements. The result is in line with a handful of recent empirical studies reporting that RP changes as a function of task (Pinheiro, Schwartz, Amorim, et al., 2020; Pinheiro, Schwartz, Gutiérrez-Domínguez, & Kotz, 2020; Reznik et al., 2018; Vercillo et al., 2018). Together with these studies, it also corroborates the functional characterization of the RP within the framework of the motor control theories.

According to the forward model of motor control, voluntary (active) movements are accompanied by an efference copy which contains a prediction for the upcoming sensory consequences associated with that action. Such a prediction would not be present when a movement is passively executed. Prior studies have exclusively investigated RPs preceding active movements (Pinheiro, Schwartz, Amorim, et al., 2020; Pinheiro, Schwartz, Gutiérrez-Domínguez, & Kotz, 2020; Reznik et al., 2018; Vercillo et al., 2018; Wen et al., 2018). Our results complement these by implementing a passive condition to control for proprioceptive feedback. Using this method, we found clear differences *between* the movement types for at least both the visual and auditory conditions. In other words, when

expecting an immediate sensory outcome, RP was different during the preparation of active and passive movements. This supports the notion of an efference-copy-based forward model mechanism that predicts the sensory consequences of actions.

In the control condition, where the feedback was delayed by 1 s, there was moderate evidence of no difference between active and passive movements. It should be noted that this condition was not devoid of sensory feedback, as there was still tactile and proprioceptive information associated with the button presses. However, the design allows for optimal control over these factors, since they are present in both movement types, unlike with a completely passively presented stimulus. However, it could be argued that there should be an effect of additional predictive processes in the active control condition, in spite of the lack of an immediately associated visual or auditory action effect. This result could be interpreted within the framework of the common coding principle (Hommel et al., 2001; Roussel et al., 2013). According to this theory, when an action consistently leads to a sensory consequence, an association is made between the action and the sensory outcome, forming a shared representational code. Therefore, perceiving an action effect involves the same internal representation as performing the action and vice versa. It is possible that the active movements formed a representational code along with the visual or auditory stimuli that they were associated with. However, the passive movements, being involuntary, did not form such an association, leading to the differences between the conditions. Likewise, the control conditions trigger immediate auditory or visual sensations and therefore, neither the active nor the passive condition would have formed this association. Previous reports have shown that expected sensory feedback is represented in the RP (Pinheiro, Schwartz, Amorim, et al., 2020; Pinheiro, Schwartz, Gutiérrez-Domínguez, & Kotz, 2020; Reznik et al., 2018; Vercillo et al., 2018; Wen et al., 2018). The results presented here significantly extend this, using the higher-level baseline provided by passive movements.

RPs have been recorded preceding actions associated with sensory consequences in different sensory modalities, such as visual (Bianco et al., 2020; Vercillo et al., 2018) and auditory (Jahanshahi et al., 1995; Pinheiro, Schwartz, Amorim, et al., 2020; Pinheiro, Schwartz, Gutiérrez-Domínguez, & Kotz, 2020; Reznik et al., 2018). However, there is little evidence to suggest whether or not the RP encodes the sensory modality of the action's consequences. In one experiment by Bianco et al. (2020), the authors suggested that the RP does not encode the sensory modality, once the influence of preparatory ERPs related to perceiving the stimulus alone (with no movement) has been subtracted. To investigate whether the RP encoded the upcoming stimulus modality, we performed a follow-up analysis, which included only the conditions where a stimulus followed the button press (see Supplement). There was no interaction between modality and movement type, suggesting that the differences between active and passive movements were similar across modalities. This was corroborated in the DAT analysis, where no significant differences were observed between the auditory and visual conditions. In short, we conclude here that motor-preparatory EEG

signals do not differ when expecting a visual versus an auditory stimulus.

4.2 | LRP as a functional neural marker for motor preparation

While the RP is thought to reflect general preparation for upcoming movements, LRP is considered to represent motor-specific preparation, occurring in the primary motor cortex (M1), due to its lateralization (Brunia et al., 2012; Smulders & Miller, 2012). In our experiment, we expected that there should be greater LRP amplitudes for the active condition, as motor-specific preparation would be absent in the passive condition. All active conditions showed a similar sharp decrease in LRP amplitude shortly before the button press that was not present in the passive conditions, suggesting that there was motor-specific preparation in active but not the passive conditions. Furthermore, there was strong evidence that the LRP was not different between task conditions, providing additional support that this potential is specific to motor preparation and does not encode action-effect contingency. Previous studies have found inconsistent results for the role of LRP in encoding stimulus expectancy. Some studies have found that LRP does not encode action-effect contingency (Reznik et al., 2018; Vercillo et al., 2018), while others have suggested that LRP does contain this information (Ford et al., 2014; Hughes & Waszak, 2011). However, these prior studies only considered low- and high-level motor contributions *separately*. With our design, we took both factors into account at the same time, providing good evidence for dissociative roles of the RP and LRP in high- and low-level motor processes. Additionally, it seems intuitive that the LRP should be absent before involuntary movements (as shown in Figure 3b). However, to our knowledge, there have been no other studies to date which directly tested this assumption by comparing voluntary and involuntary movements. Future studies could complement this finding by examining activity preceding voluntary and involuntary movements in different motor areas using a technique with higher spatial resolution, such as fMRI.

4.3 | Going beyond univariate markers of movement preparation

For the first time, in addition to the univariate RP and LRP analyses, we employed an MVPA approach to investigate action effect contingency in pre-movement neural activity. First, we trained the classifier to decode active and passive movements before the movement onset and tested whether decoding varied as a function of task. Our results largely corroborate what has been observed in the RP data. However, they also offer several additional perspectives.

In the DAT, decoding accuracy for active versus passive movements increased from chance level in the baseline period to close to 90% accuracy at the time of the button press. This was not only the case for the visual and auditory conditions but also the control

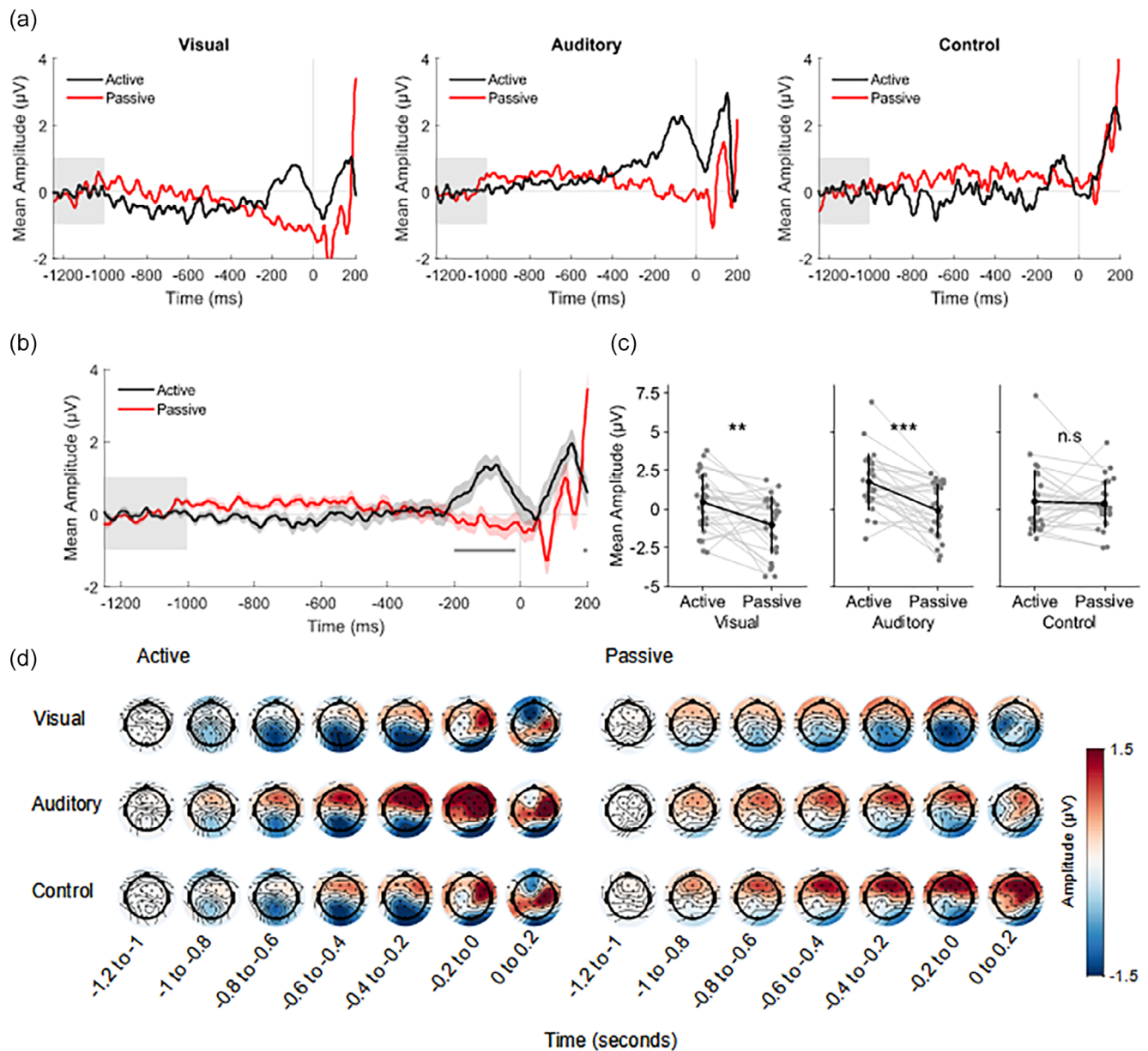


FIGURE 3 Readiness potential. (a) Average of electrodes Cz, C3, and C4, time-locked to the button press ($t = 0$). The grey shaded area denotes the baseline period. (b) Average of Cz, C3, and C4 across all task conditions (visual, auditory, control) for the active and passive movements. The grey shaded area denotes the baseline period. The grey horizontal bars show two significant clusters identified by the permutation test. The coloured shaded areas around the ERPs show the standard error. (c) Mean amplitudes averaged across the significant time points, before button press only, as identified in the permutation test (as shown in panel b). Grey points show individual participants while the black points show the group mean. $*p < .05$, $**p < .01$, $*p < .001$. Significance indicators are based on post hoc comparisons. (d) Topographical plots for all experimental conditions.

condition. This finding largely coincides with what we observed from the RP data for the visual and the auditory task. However, while the difference between movement types in the control condition was not visible in the RP, the DAT clearly showed that these two conditions can be differentiated when taking into account patterns of activity across the whole scalp. As a method with increased sensitivity (Grootswagers et al., 2017; He et al., 2022), MVPA detects the nuanced neural differences between active and passive control conditions, which might be hidden in the RP. In other

words, the motor preparatory neural activity still differs, but this difference is merely not represented in the RP. Future experiments will be necessary to examine the exact underlying neural basis for this difference.

Despite being discernible only from the MVPA analysis, we nonetheless observed significantly lower decoding performance in the control condition compared to the visual and auditory conditions in the time window beginning around 200 ms before the button press. This result is remarkably consistent with the RP. With two

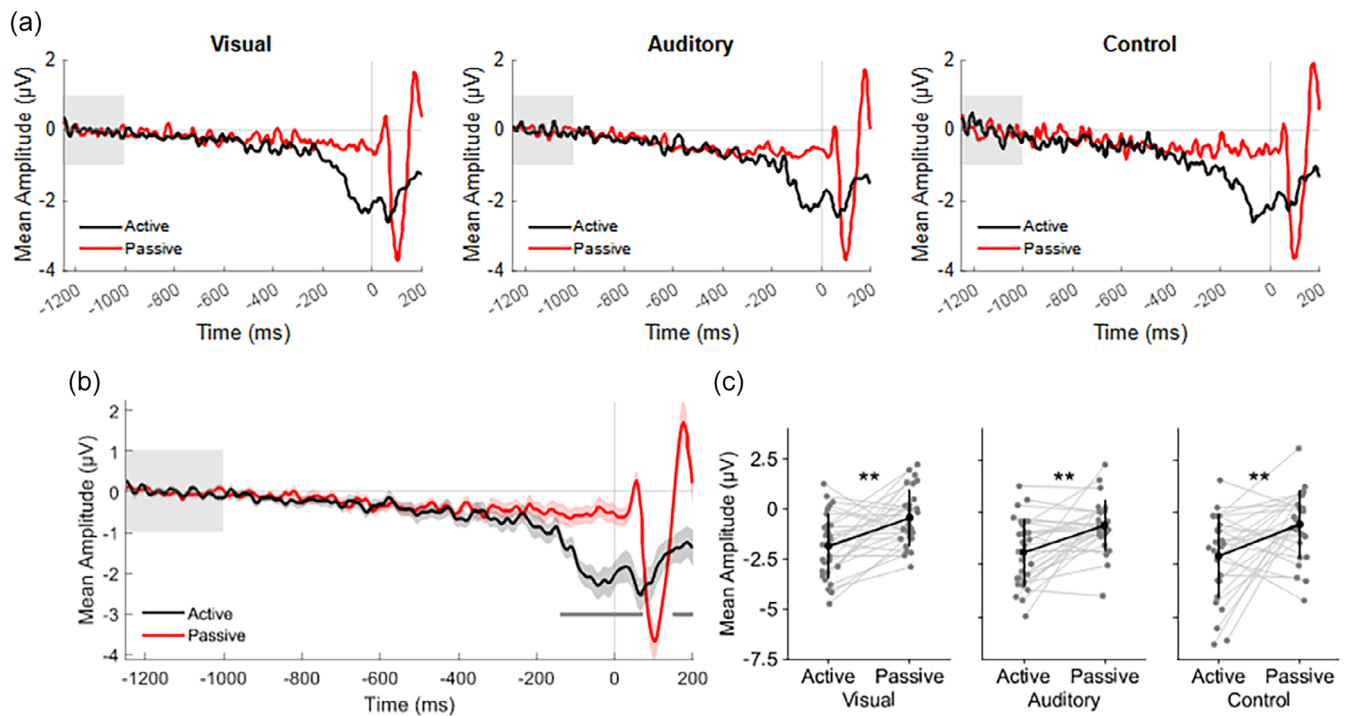


FIGURE 4 Lateralized readiness potentials. (a) Average of C3–C4, time-locked to the button press ($t = 0$). The grey shaded area denotes the baseline period. (b) Average of C3–C4 across all task conditions (visual, auditory, control) for the active and passive movements. The grey shaded area denotes the baseline period. The grey horizontal bars show two significant clusters identified by the permutation test. The coloured shaded areas around the ERPs show the standard error. (c) Mean amplitudes averaged across the significant time points, before button press only, identified in the permutation test. $*p < .05$, $**p < .01$, $*p < .001$. Significance indicators are based on the main effect of movement. Grey points show individual participants while the black points show the group mean.

fundamentally distinctive data analysis techniques, we observed converging evidence for larger differences between movement types when the movements were followed by the stimulus. In the motor control condition, the action effect was delayed by 1000 ms, lowering the contingency between the action and its effect and therefore the subjective feeling of agency over the action feedback (Wen, 2019). The pattern could be explained by additional action-effect prediction for the self-generated visual and auditory stimuli, making the movement type easier to decode in these conditions compared to the control condition, where the action effects were not as contingent.

We also conducted an analysis from another angle, training the classifier to decode sensory modality (visual vs. auditory) for the active and passive conditions. This analysis was consistent with the first, showing ramping decoding in the active and passive conditions. Interestingly, the active condition showed significantly higher decoding accuracy shortly (approximately 180 ms) before the button press. One way to interpret this result is as perceptual sharpening (Yon et al., 2018, 2023). This theory states that activity within sensory regions is weighted towards outcomes that are expected based on prior experiences. Activity in populations tuned towards expected outcomes is increased and those tuned towards unexpected outcomes is suppressed. This means there is a better signal-to-noise ratio for expected outcomes, which in turn would lead to better decoding performance by the classifier. Our results are consistent with this

theory, as according to the efference copy-based forward model theory, self-generated actions are preceded by stronger predictions. While previous studies (Yon et al., 2018, 2023) have shown enhanced decoding for expected action outcomes, our results suggest that the sharpening also occurs before the action outcome has been presented. Another interpretation is the preactivation account of sensory attenuation (Roussel et al., 2013; Waszak et al., 2012). Under this theory, when an action is voluntary, the action and its outcome form a bidirectional association which activates a common representational code for the action and its sensory consequences. Once this association is formed, the common representation is activated before the movement. This would increase the signal above the noise, thus increasing the signal-to-noise ratio and improving the performance of the classifier. Both of these therefore theories arrive at greater signal-to-noise ratios but through different processes. With the current data, we cannot disentangle these two possibilities but this could be an interesting question for future studies.

In the present study, expectancy was manipulated by changing whether the action outcome was self- or externally generated. It would be an interesting question for future studies to investigate whether there is higher decoding accuracy *before* a movement for stimuli where the expectancy is manipulated in a different way, such as establishing and then changing an action-outcome association.

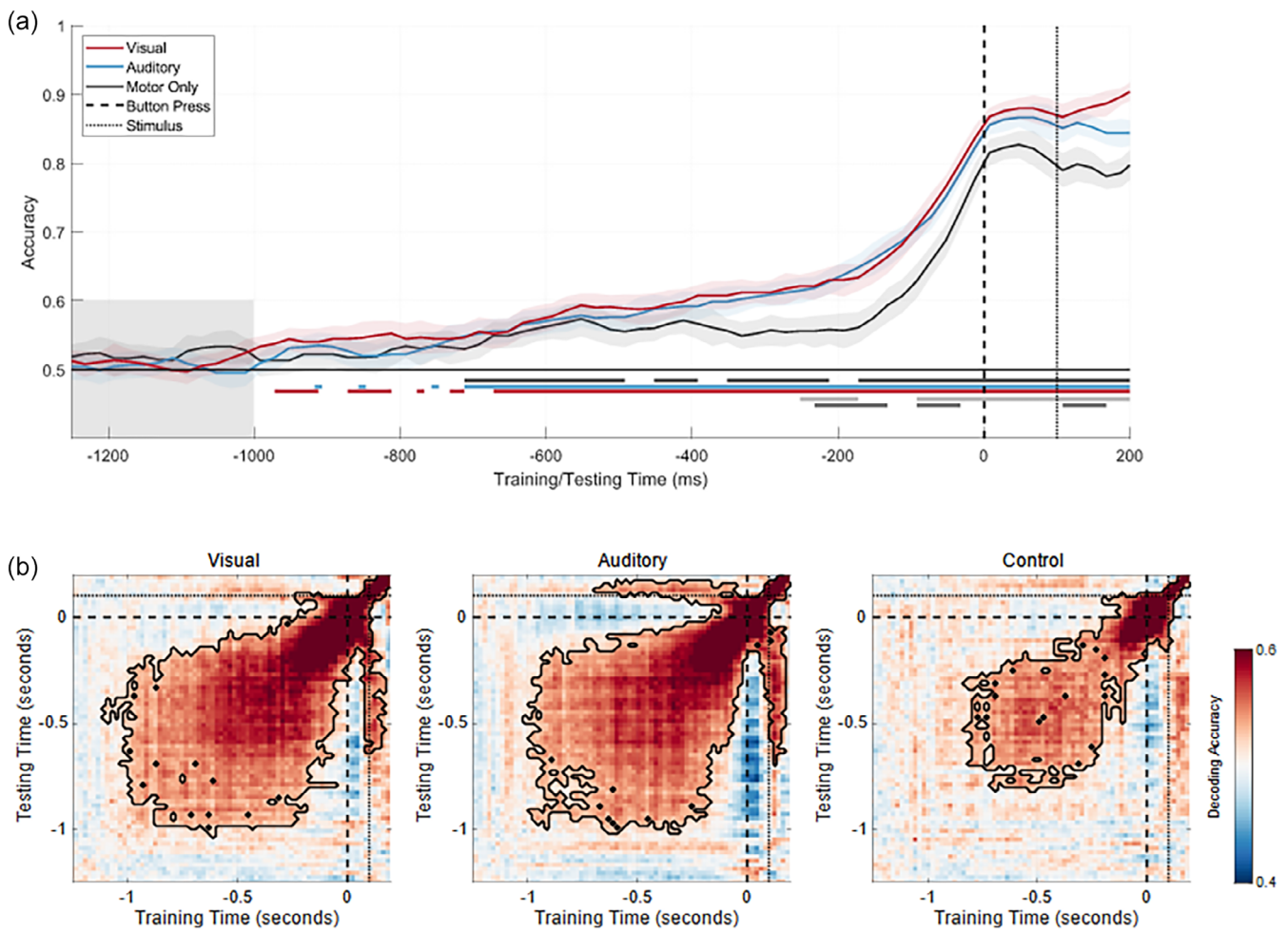


FIGURE 5 Multivariate pattern analysis (MVPA) results for decoding active and passive movements. (a) Decoding across time results, showing mean decoding accuracy (active vs. passive movement) at each time point. The grey shaded area denotes the baseline period. The coloured shaded areas around the curves show the standard error. The horizontal bars corresponding to the colours of the curves show clusters where those conditions significantly ($p < .05$) differed from chance level decoding (0.5). The light grey horizontal bar shows clusters where the visual and control conditions differed significantly ($p < .05$, corrected). The dark grey horizontal bar shows clusters where the auditory and control conditions differed significantly ($p < .05$, corrected). (b) Temporal generalisation matrices. Classifiers are trained at time point t_0 (x-axis) and tested at all time points (y-axis). Warmer colours indicate higher decoding accuracy. The outlined contours show where decoding accuracy is significantly ($p < .05$) above chance level (0.5).

While previous studies have suggested distinct phases for the RP (Brunia et al., 2012; Jo et al., 2014; Pinheiro, Schwartz, Gutiérrez-Domínguez, & Kotz, 2020; Vercillo et al., 2018; Wen et al., 2018), we did not find evidence for this in our results. In the RP analysis, only the later phase (around 200 ms before the button press) differed between movement types. These data pattern appears to be consistent with the observed ramping pattern of the decoding time series across conditions as revealed in DAT, where decoding performance starts to peak also from -200 ms onwards. We then examined the TG matrices for evidence of distinct phases of processing. This approach offers the opportunity to reveal dynamics of brain activity and specifically how temporally distinctive processes are related to each other (J. R. King & Dehaene, 2014). The results presented here suggest that the late and the early time windows may be supported by a shared, single neurocognitive process, which begins around 1000 ms before

the button press and slowly ramps up before the movement. This stands in contrast to the traditional view of the RP as comprising two separate phases (Shibasaki & Hallett, 2006). Moreover, despite differences between the visual/auditory and control conditions, all three conditions were cross-decodable, implying that their neural basis is similar (see Supplement).

4.4 | Limitations

In the context of human volition and consciousness, voluntary actions are considered to be stimulus-independent (Haggard, 2008), making them difficult to produce in laboratory settings. Previous studies have circumvented this issue by having the participant choose either whether or not to perform an action, which action to perform or how

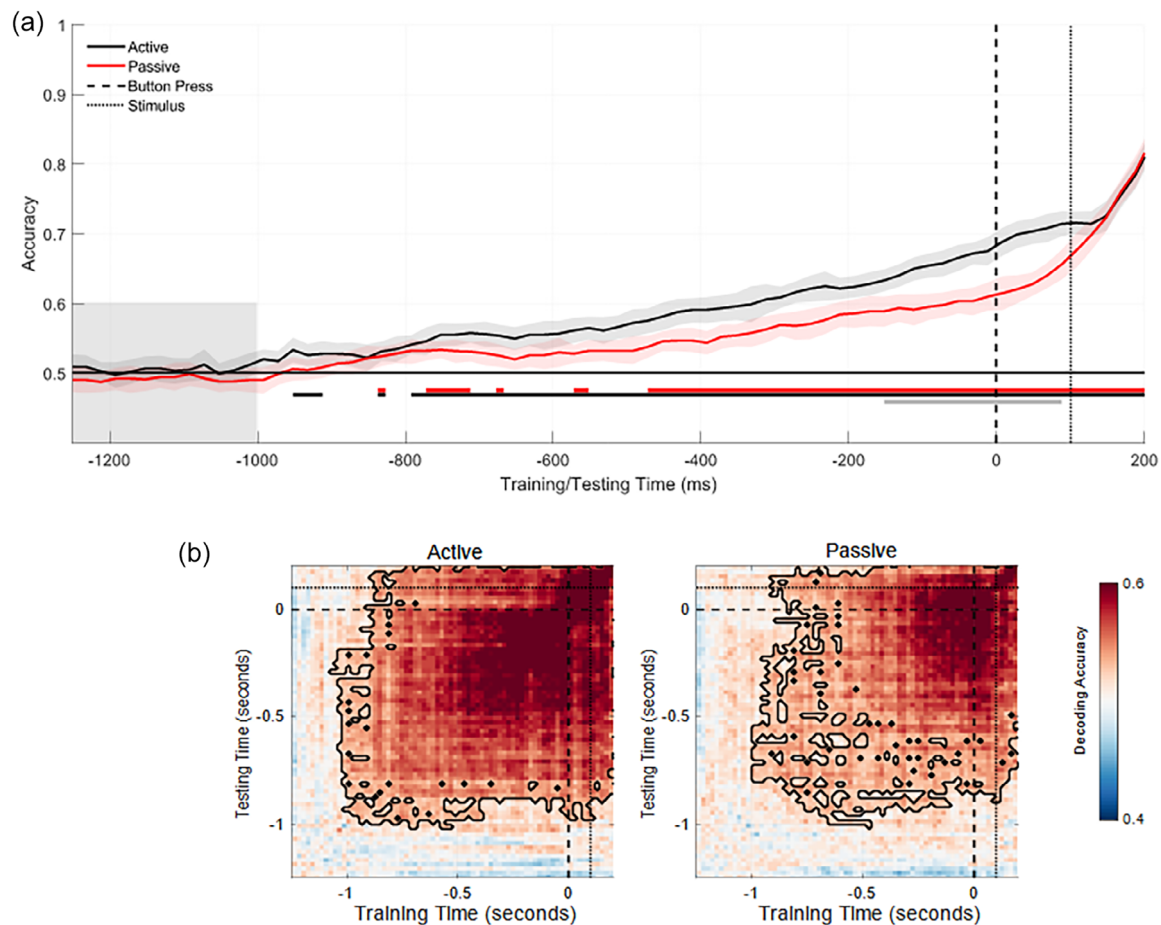


FIGURE 6 Multivariate pattern analysis (MVPA) results for decoding visual and auditory sensory modality. (a) Decoding across time results, showing mean decoding accuracy (visual vs. auditory) at each time point. The grey shaded area denotes the baseline period. The coloured shaded areas around the curves show the standard error. The horizontal bars corresponding to the colours of the curves show clusters where those conditions significantly ($p < .05$) differed from chance level decoding (0.5). The light grey horizontal bar shows clusters where the visual and control conditions differed significantly ($p < .05$). The dark grey horizontal bar shows clusters where the auditory and control conditions differed significantly ($p < .05$, corrected). (b) Temporal generalisation matrices. Classifiers are trained at time point t_0 (x-axis) and tested at all time points (y-axis). Warmer colours indicate higher decoding accuracy. The outlined contours show where decoding accuracy is significantly ($p < .05$) above chance level (0.5).

many actions to perform. In most studies, however, there is still not any reason that participants should be motivated to choose one movement over another. One potential limitation of this study is that the active movements would not be considered completely voluntary under this strict definition. However, they clearly differ from the passive movements, which require no planning for their execution, a notion which is corroborated by our results. Previous studies have shown that voluntary and stimulus-driven movements differ in the cortical resources recruited during their planning and execution (Cunnington et al., 1995; Jahanshahi et al., 1995; Papa et al., 1991). Therefore, future studies should consider different classes of movements (e.g., voluntary vs. stimulus-driven) when investigating pre-movement neural activity in the context of self- and externally generated sensations.

In our study, the RPs did not show a slow-rising negative morphology as reported in some other studies. It is possible that these data pattern was obscured by the high-level processes that were of

interest in this study. One piece of evidence for this is that we observed relatively more typical LRPs. The subtraction procedure that is used to derive the LRP may have eliminated the influence of non-motor factors which do not contribute to lateralization. Furthermore, Trovò et al. (2021) found that the RP lacked the typical negative shape, instead being positive or absent in around half of their participants.

One limitation of the current design is that the distribution of time durations between the cue onset and the button press was different between the active and passive conditions. We did not place any restrictions on the time of the button presses in the active condition, instead allowing the movements to be self-paced. However, this meant that the button presses were quicker in the active conditions than in the passive condition. An alternative design that could be used in future studies would be to match the time durations by recording them in the active condition and using these in the passive condition. However, this design would mean

that the active condition always has to be presented first and does not allow for counterbalancing.

5 | CONCLUSION

Evidence from previous studies shows that pre-motor ERPs encode expectations for action effects. The current study circumvented caveats of previous investigations by manipulating movement type and action-effect contingency within a single design. Taken together, the results suggest that the brain anticipates the sensory consequences of voluntary actions and support the notion of dissociative roles for the RP and LRP. Our RP findings suggest that motor preparation areas are involved in the expectation of upcoming sensory consequences, and that these predictive processes are reduced for passive movements. Conversely, the LRP does not encode task and instead shows differences purely related to the movement. The DAT results suggest that predictive processes are not limited to central electrode locations but are distributed across the entire scalp. Finally, we did not find evidence for distinct early and late phases of processing. Rather, the time generalisation showed a single ramping process, homogenous between visual, auditory and control beginning around 1000 ms before the button press. Overall, these results provide novel evidence of an efference copy-based forward model mechanism being already represented in the pre-motor neural activity.

ACKNOWLEDGEMENT

The authors thank Katharina Schuster and Mona Rauschkolb for assistance with data collection and translation and Ruslan Spartakov and Julia Oppermann for assistance with data collection. Open Access funding enabled and organized by Projekt DEAL.

FUNDING INFORMATION

This work was supported by Deutsche Forschungsgemeinschaft (STR 1146/9-1/2, grant number 286893149; SFB/TRR 135 TP A3: 'Cardinal mechanisms of perception: prediction, valuation, categorization', grant number 222641018; GRK 1901/2, IRTG 1901 "The Brain in Action"). This work was further supported by the Hessisches Ministerium für Wissenschaft und Kunst (HMWK; project "The Adaptive Mind"). The funders had no role in the study design, collection or analysis of data, writing or the decision to publish the article.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Group-level data and accompanying scripts supporting the conclusion presented in this study are available from OSF: DOI [10.17605/OSF.IO/3QFXB](https://doi.org/10.17605/OSF.IO/3QFXB).

ORCID

Edward Ody  <https://orcid.org/0000-0001-7198-9205>

REFERENCES

- Andraszewicz, S., Scheibehenne, B., Rieskamp, J., Grasman, R., Verhagen, J., & Wagenmakers, E.-J. (2015). An introduction to Bayesian hypothesis testing for management research. *Journal of Management*, 41(2), 521–543. <https://doi.org/10.1177/0149206314560412>
- Arikan, B. E., van Kemenade, B. M., Straube, B., Harris, L. R., & Kircher, T. (2017). Voluntary and involuntary movements widen the window of subjective simultaneity. *I-Perception*, 8(4), 204166951771929. <https://doi.org/10.1177/2041669517719297>
- Arikan, B. E., van Kemenade, B. M. V., Podranski, K., Steinräter, O., Straube, B., & Kircher, T. (2019). Perceiving your hand moving: BOLD suppression in sensory cortices and the role of the cerebellum in the detection of feedback delays. *Journal of Vision*, 19(14), 1–22. <https://doi.org/10.1167/19.14.4>
- Baess, P., Horváth, J., Jacobsen, T., & Schröger, E. (2011). Selective suppression of self-initiated sounds in an auditory stream: An ERP study. *Psychophysiology*, 48(9), 1276–1283. <https://doi.org/10.1111/j.1469-8986.2011.01196.x>
- Bansal, S., Ford, J. M., & Spering, M. (2018). The function and failure of sensory predictions. *Annals of the New York Academy of Sciences*, 1426, 199–220. <https://doi.org/10.1111/nyas.13686>
- Bäß, P., Jacobsen, T., & Schröger, E. (2008). Suppression of the auditory N1 event-related potential component with unpredictable self-initiated tones: Evidence for internal forward models with dynamic stimulation. *International Journal of Psychophysiology*, 70(2), 137–143. <https://doi.org/10.1016/j.ijpsycho.2008.06.005>
- Bianco, V., Berchicci, M., Livio Perri, R., Quinzi, F., Mussini, E., Spinelli, D., & Di Russo, F. (2020). Preparatory ERPs in visual, auditory, and somatosensory discriminative motor tasks. *Psychophysiology*, 57(12), e13687. <https://doi.org/10.1111/psyp.13687>
- Blakemore, S. J., & Frith, C. (2003). Self-awareness and action. *Current Opinion in Neurobiology*, 13(2), 219–224. [https://doi.org/10.1016/S0959-4388\(03\)00043-6](https://doi.org/10.1016/S0959-4388(03)00043-6)
- Brunia, C. H. M., van Boxtel, G. J. M., & Böcker, K. B. E. (2012). Negative slow waves as indices of anticipation: The Bereitschaftspotential, the contingent negative variation, and the stimulus-preceding negativity. In *The Oxford handbook of event-related potential components* (Vol. 1–22). Oxford University Press. <https://doi.org/10.1093/oxfordhb/9780195374148.013.0108>
- Carlson, T., Tovar, D. A., Alink, A., & Kriegeskorte, N. (2013). Representational dynamics of object vision: The first 1000 ms. *Journal of Vision*, 13(10), 1–19. <https://doi.org/10.1167/13.10.1>
- Cunnington, R., Iansek, R., Bradshaw, J. L., & Phillips, J. G. (1995). Movement-related potentials in Parkinson's disease. Presence and predictability of temporal and spatial cues. *Brain*, 118(Pt 4), 935–950. <https://doi.org/10.1093/brain/118.4.935>
- Deecke, L. (1987). Bereitschaftspotential as an indicator of movement preparation in supplementary motor area and motor cortex. *Ciba Foundation Symposium*, 132, 231–250. <https://doi.org/10.1002/9780470513545.ch14>
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134(1), 9–21. <https://doi.org/10.1016/j.jneumeth.2003.10.009>
- Ford, J. M., Palzes, V. A., Roach, B. J., & Mathalon, D. H. (2014). Did I do that? Abnormal predictive processes in schizophrenia when button pressing to deliver a tone. *Schizophrenia Bulletin*, 40(4), 804–812. <https://doi.org/10.1093/schbul/sbt072>
- Fried, I., Mukamel, R., & Kreiman, G. (2011). Internally generated preactivation of single neurons in human medial frontal cortex predicts volition. *Neuron*, 69(3), 548–562. <https://doi.org/10.1016/j.neuron.2010.11.045>
- Fuehrer, E., Voudouris, D., Lezkan, A., Drewing, K., & Fiehler, K. (2022). Tactile suppression stems from specific sensorimotor predictions. *Proceedings of the National Academy of Sciences of the United States of*

- America, 119(20), e2118445119. <https://doi.org/10.1073/pnas.2118445119>
- Gerber, E. M. (2023). permutest. Retrieved from <https://www.mathworks.com/matlabcentral/fileexchange/71737-permutest>
- Gratton, G., Coles, M. G., Sirevaag, E. J., Eriksen, C. W., & Donchin, E. (1988). Pre- and poststimulus activation of response channels: A psychophysiological analysis. *Journal of Experimental Psychology. Human Perception and Performance*, 14(3), 331–344. <https://doi.org/10.1037//0096-1523.14.3.331>
- Grootswagers, T., Wardle, S. G., & Carlson, T. A. (2017). Decoding dynamic brain patterns from evoked responses: A tutorial on multivariate pattern analysis applied to time series neuroimaging data. *Journal of Cognitive Neuroscience*, 29(4), 677–697. https://doi.org/10.1162/jocn_a_01068
- Haggard, P. (2008). Human volition: Towards a neuroscience of will. *Nature Reviews. Neuroscience*, 9(12), 934–946. <https://doi.org/10.1038/nrn2497>
- Haggard, P., & Whitford, B. (2004). Supplementary motor area provides an efferent signal for sensory suppression. *Brain Research. Cognitive Brain Research*, 19(1), 52–58. <https://doi.org/10.1016/j.cogbrainres.2003.10.018>
- Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science*, 293(5539), 2425–2430. <https://doi.org/10.1126/science.1063736>
- He, Y., Sommer, J., Hansen-Schirra, S., & Nagels, A. (2022). Negation impacts sentence processing in the N400 and later time windows: Evidence from multivariate pattern analysis of EEG. Retrieved from <https://psyarxiv.com/8rbw3/download?format=pdf>
- Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The theory of event coding (TEC): A framework for perception and action planning. *The Behavioral and Brain Sciences*, 24(5), 849–878. <https://doi.org/10.1017/s0140525X01000103>
- Hughes, G., & Waszak, F. (2011). ERP correlates of action effect prediction and visual sensory attenuation in voluntary action. *NeuroImage*, 56(3), 1632–1640. <https://doi.org/10.1016/j.neuroimage.2011.02.057>
- Ikeda, A., Lüders, H. O., Burgess, R. C., & Shibasaki, H. (1992). Movement-related potentials recorded from supplementary motor area and primary motor area. Role of supplementary motor area in voluntary movements. *Brain*, 115(Pt 4), 1017–1043. <https://doi.org/10.1093/brain/115.4.1017>
- Jahanshahi, M., Jenkins, I. H., Brown, R. G., Marsden, C. D., Passingham, R. E., & Brooks, D. J. (1995). Self-initiated versus externally triggered movements. I. An investigation using measurement of regional cerebral blood flow with PET and movement-related potentials in normal and Parkinson's disease subjects. *Brain*, 118(Pt 4), 913–933. <https://doi.org/10.1093/brain/118.4.913>
- Jo, H.-G., Wittmann, M., Hinterberger, T., & Schmidt, S. (2014). The readiness potential reflects intentional binding. *Frontiers in Human Neuroscience*, 8, 421. <https://doi.org/10.3389/fnhum.2014.00421>
- Keyser, C., Gazzola, V., & Wagenmakers, E.-J. (2020). Author correction: Using Bayes factor hypothesis testing in neuroscience to establish evidence of absence. *Nature Neuroscience*, 23(11), 1453. <https://doi.org/10.1038/s41593-020-00710-7>
- King, J. R., & Dehaene, S. (2014). Characterizing the dynamics of mental representations: The temporal generalization method. *Trends in Cognitive Sciences*, 18(4), 203–210. <https://doi.org/10.1016/j.tics.2014.01.002>
- King, J.-R., Gramfort, A., Schurger, A., Naccache, L., & Dehaene, S. (2014). Two distinct dynamic modes subtend the detection of unexpected sounds. *PLoS One*, 9(1), e85791. <https://doi.org/10.1371/journal.pone.0085791>
- Klug, M., & Kloosterman, N. A. (2022). Zapline-plus: A Zapline extension for automatic and adaptive removal of frequency-specific noise artifacts in M/EEG. *Human Brain Mapping*, 43(9), 2743–2758. <https://doi.org/10.1002/hbm.25832>
- Kornhuber, H. H., & Deecke, L. (2016). Brain potential changes in voluntary and passive movements in humans: Readiness potential and reafferent potentials. *Pflügers Archiv: European Journal of Physiology*, 468(7), 1115–1124. <https://doi.org/10.1007/s00424-016-1852-3>
- Kutas, M., & Donchin, E. (1980). Preparation to respond as manifested by movement-related brain potentials. *Brain Research*, 202(1), 95–115.
- Ledoit, O., & Wolf, M. (2004). Honey, I shrunk the sample covariance matrix. *Journal of Portfolio Management*, 691, 110–119. Retrieved from <https://jpm.pm-research.com/content/30/4/110.short>
- Li, Q., Wang, J., Li, Z., & Chen, A. (2022). Decoding the specificity of post-error adjustments using EEG-based multivariate pattern analysis. *The Journal of Neuroscience*, 42(35), 6800–6809. <https://doi.org/10.1523/JNEUROSCI.0590-22.2022>
- Love, J., Selker, R., Marsman, M., Jamil, T., Dropmann, D., Verhagen, J., Ly, A., Gronau, Q. F., Šmíra, M., Epskamp, S., Matzke, D., Wild, A., Knight, P., Rouder, J. N., Morey, R. D., & Wagenmakers, E.-J. (2019). JASP: Graphical statistical software for common statistical designs. *Journal of Statistical Software*, 88, 1–17. <https://doi.org/10.18637/jss.v088.i02>
- Lubinus, C., Einhäuser, W., Schiller, F., Kircher, T., Straube, B., & van Kemenade, B. M. (2022). Action-based predictions affect visual perception, neural processing, and pupil size, regardless of temporal predictability. *NeuroImage*, 263, 119601. <https://doi.org/10.1016/j.neuroimage.2022.119601>
- Martikainen, M. H., Kaneko, K.-I., & Hari, R. (2005). Suppressed responses to self-triggered sounds in the human auditory cortex. *Cerebral Cortex*, 15(3), 299–302. <https://doi.org/10.1093/cercor/bhh131>
- McLachlan, G. J. (2005). *Discriminant analysis and statistical pattern recognition*. John Wiley & Sons. Retrieved from https://play.google.com/store/books/details?id=O_qHDLaWpDUC
- Mifsud, N. G., Oestreich, L. K. L., Jack, B. N., Ford, J. M., Roach, B. J., Mathalon, D. H., & Whitford, T. J. (2016). Self-initiated actions result in suppressed auditory but amplified visual evoked components in healthy participants. *Psychophysiology*, 53(5), 723–732. <https://doi.org/10.1111/psyp.12605>
- Ody, E., Straube, B., He, Y., & Kircher, T. (2023). Perception of self-generated and externally-generated visual stimuli: Evidence from EEG and behavior. *Psychophysiology*, 60, e14295. <https://doi.org/10.1111/psyp.14295>
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, 2011, 156869. <https://doi.org/10.1155/2011/156869>
- Papa, S. M., Artieda, J., & Obeso, J. A. (1991). Cortical activity preceding self-initiated and externally triggered voluntary movement. *Movement Disorders*, 6(3), 217–224. <https://doi.org/10.1002/mds.870060305>
- Pazen, M., Uhlmann, L., van Kemenade, B. M., Steinsträter, O., Straube, B., & Kircher, T. (2020). Predictive perception of self-generated movements: Commonalities and differences in the neural processing of tool and hand actions. *NeuroImage*, 206(August), 116309. <https://doi.org/10.1016/j.neuroimage.2019.116309>
- Pinheiro, A. P., Schwartz, M., Amorim, M., Coentre, R., Levy, P., & Kotz, S. A. (2020). Changes in motor preparation affect the sensory consequences of voice production in voice hearers. *Neuropsychologia*, 146(January), 107531. <https://doi.org/10.1016/j.neuropsychologia.2020.107531>
- Pinheiro, A. P., Schwartz, M., Gutiérrez-Domínguez, F., & Kotz, S. A. (2020). Real and imagined sensory feedback have comparable effects on action anticipation. *Cortex*, 130, 290–301. <https://doi.org/10.1016/j.cortex.2020.04.030>
- Pion-Tonachini, L., Kreutz-Delgado, K., & Makeig, S. (2019). ICLLabel: An automated electroencephalographic independent component classifier, dataset, and website. *NeuroImage*, 198, 181–197. <https://doi.org/10.1016/j.neuroimage.2019.05.026>

- Praamstra, P., Stegeman, D. F., Horstink, M. W., & Cools, A. R. (1996). Dipole source analysis suggests selective modulation of the supplementary motor area contribution to the readiness potential. *Electroencephalography and Clinical Neurophysiology*, 98(6), 468–477. [https://doi.org/10.1016/0013-4694\(96\)95643-6](https://doi.org/10.1016/0013-4694(96)95643-6)
- Press, C., Kok, P., & Yon, D. (2020). The perceptual prediction paradox. *Trends in Cognitive Sciences*, 24(1), 13–24. <https://doi.org/10.1016/j.tics.2019.11.003>
- Rektor, I., Fève, A., Buser, P., Bathien, N., & Lamarche, M. (1994). Intracerebral recording of movement related readiness potentials: An exploration in epileptic patients. *Electroencephalography and Clinical Neurophysiology*, 90(4), 273–283. [https://doi.org/10.1016/0013-4694\(94\)90145-7](https://doi.org/10.1016/0013-4694(94)90145-7)
- Reznik, D., Guttman, N., Buaron, B., Zion-Golumbic, E., & Mukamel, R. (2021). Action-locked neural responses in auditory cortex to self-generated sounds. *Cerebral Cortex*, 31(12), 5560–5569. <https://doi.org/10.1093/cercor/bhab179>
- Reznik, D., Simon, S., & Mukamel, R. (2018). Predicted sensory consequences of voluntary actions modulate amplitude of preceding readiness potentials. *Neuropsychologia*, 119, 302–307. <https://doi.org/10.1016/j.neuropsychologia.2018.08.028>
- Roussel, C., Hughes, G., & Waszak, F. (2013). A preactivation account of sensory attenuation. *Neuropsychologia*, 51(5), 922–929. <https://doi.org/10.1016/j.neuropsychologia.2013.02.005>
- Sanmiguel, I., Todd, J., & Schröger, E. (2013). Sensory suppression effects to self-initiated sounds reflect the attenuation of the unspecific N1 component of the auditory ERP. *Psychophysiology*, 50(4), 334–343. <https://doi.org/10.1111/psyp.12024>
- Schaefer, R. S., Farquhar, J., Blokland, Y., Sadakata, M., & Desain, P. (2011). Name that tune: Decoding music from the listening brain. *NeuroImage*, 56(2), 843–849. <https://doi.org/10.1016/j.neuroimage.2010.05.084>
- Schmitter, C. V., Steinsträter, O., Kircher, T., van Kemenade, B. M., & Straube, B. (2021). Commonalities and differences in predictive neural processing of discrete vs continuous action feedback. *NeuroImage*, 229(July 2020), 117745. <https://doi.org/10.1016/j.neuroimage.2021.117745>
- Schmitter, C. V., & Straube, B. (2022). The impact of cerebellar transcranial direct current stimulation (tDCS) on sensorimotor and inter-sensory temporal recalibration. *Frontiers in Human Neuroscience*, 16(August), 998843. <https://doi.org/10.3389/fnhum.2022.998843>
- Shibasaki, H., & Hallett, M. (2006). What is the Bereitschaftspotential? *Clinical Neurophysiology*, 117(11), 2341–2356. <https://doi.org/10.1016/j.clinph.2006.04.025>
- Smulders, F. T. Y., & Miller, J. O. (2012). The lateralized readiness potential. In *The Oxford handbook of event-related potential components* (Vol. 1980, pp. 1–24). Oxford University Press. <https://doi.org/10.1093/oxfordhb/9780195374148.013.0115>
- Straube, B., Van Kemenade, B. M., Arikan, B. E., Fiehler, K., Leube, D. T., Harris, L. R., & Kircher, T. (2017). Predicting the multisensory consequences of one's own action: Bold suppression in auditory and visual cortices. *PLoS One*, 12(1), 1–25. <https://doi.org/10.1371/journal.pone.0169131>
- Straube, B., van Kemenade, B. M., Kircher, T., & Schülke, R. (2020). Transcranial direct current stimulation improves action-outcome monitoring in schizophrenia spectrum disorder. *Brain Communications*, 2(2), 1–16. <https://doi.org/10.1093/braincomms/fcaa151>
- Treder, M. S. (2020). MVPA-light: A classification and regression toolbox for multi-dimensional data. *Frontiers in Neuroscience*, 14(June), 1–19. <https://doi.org/10.3389/fnins.2020.00289>
- Trovò, B., Visser, Y., İşcan, Z., & Schurger, A. (2021). Movement-preceding neural activity under parametrically varying levels of time pressure. In *bioRxiv* (p. 2021.04.29.441753). <https://doi.org/10.1101/2021.04.29.441753>
- Uhlmann, L., Pazen, M., van Kemenade, B. M., Kircher, T., & Straube, B. (2021). Neural correlates of self-other distinction in patients with schizophrenia spectrum disorders: The roles of agency and hand identity. *Schizophrenia Bulletin*, 47(5), 1399–1408. <https://doi.org/10.1093/schbul/sbaa186>
- Uhlmann, L., Pazen, M., van Kemenade, B. M., Steinsträter, O., Harris, L. R., Kircher, T., & Straube, B. (2020). Seeing your own or someone else's hand moving in accordance with your action: The neural interaction of agency and hand identity. *Human Brain Mapping*, 41(9), 2474–2489. <https://doi.org/10.1002/hbm.24958>
- van Kemenade, B. M., Arikan, B. E., Kircher, T., & Straube, B. (2016). Predicting the sensory consequences of one's own action: First evidence for multisensory facilitation. *Attention, Perception & Psychophysics*, 78(8), 2515–2526. <https://doi.org/10.3758/s13414-016-1189-1>
- Vercillo, T., O'Neil, S., & Jiang, F. (2018). Action-effect contingency modulates the readiness potential. *NeuroImage*, 183, 273–279. <https://doi.org/10.1016/j.neuroimage.2018.08.028>
- von Holst, E., & Mittelstaedt, H. (1950). Das Reafferenzprinzip. *The Science of Nature*, 37(20), 464–476. <https://doi.org/10.1007/bf00622503>
- Waszak, F., Cardoso-Leite, P., & Hughes, G. (2012). Action effect anticipation: Neurophysiological basis and functional consequences. *Neuroscience and Biobehavioral Reviews*, 36(2), 943–959. <https://doi.org/10.1016/j.neubiorev.2011.11.004>
- Weiss, C., Herwig, A., & Schütz-Bosbach, S. (2011). The self in action effects: Selective attenuation of self-generated sounds. *Cognition*, 121(2), 207–218. <https://doi.org/10.1016/j.cognition.2011.06.011>
- Wen, W. (2019). Does delay in feedback diminish sense of agency? A review. *Consciousness and Cognition*, 73, 102759. <https://doi.org/10.1016/j.concog.2019.05.007>
- Wen, W., Minohara, R., Hamasaki, S., Maeda, T., An, Q., Tamura, Y., Yamakawa, H., Yamashita, A., & Asama, H. (2018). The readiness potential reflects the reliability of action consequence. *Scientific Reports*, 8(1), 11865. <https://doi.org/10.1038/s41598-018-30410-z>
- Wolpert, D. M. (1997). Computational approaches to motor control. *Trends in Cognitive Sciences*, 1(6), 209–216. [https://doi.org/10.1016/S1364-6613\(97\)01070-X](https://doi.org/10.1016/S1364-6613(97)01070-X)
- World Medical Association. (2013). World medical association declaration of Helsinki: Ethical principles for medical research involving human subjects. *JAMA*, 310(20), 2191–2194. <https://doi.org/10.1001/jama.2013.281053>
- Yon, D., Gilbert, S. J., de Lange, F. P., & Press, C. (2018). Action sharpens sensory representations of expected outcomes. *Nature Communications*, 9(1), 4288. <https://doi.org/10.1038/s41467-018-06752-7>
- Yon, D., Thomas, E. R., Gilbert, S. J., de Lange, F. P., Kok, P., & Press, C. (2023). Stubborn predictions in primary visual cortex. *Journal of Cognitive Neuroscience*, 35(7), 1133–1143.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Ody, E., Kircher, T., Straube, B., & He, Y. (2023). Pre-movement event-related potentials and multivariate pattern of EEG encode action outcome prediction. *Human Brain Mapping*, 44(17), 6198–6213. <https://doi.org/10.1002/hbm.26506>