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Illusion of control affects ERP amplitude reductions for auditory outcomes of self-generated actions

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Abstract

The reduction of neural responses to self-generated stimuli compared to external stimuli is thought to result from the matching of motor-based sensory predictions and sensory reafferences and to serve the identification of changes in the environment as caused by oneself. The amplitude of the auditory event-related potential (ERP) component N1 seems to closely reflect this matching process, while the later positive component (P2/ P3a) has been associated with judgments of agency, which are also sensitive to contextual top-down information. In this study, we examined the effect of perceived control over sound production on the processing of self-generated and external stimuli, as reflected in these components. We used a new version of a classic two-button choice task to induce different degrees of the illusion of control (IoC) and recorded ERPs for the processing of self-generated and external sounds in a subsequent task. N1 amplitudes were reduced for self-generated compared to external sounds, but not significantly affected by IoC. P2/3a amplitudes were affected by IoC: We found reduced P2/3a amplitudes after a high compared to a low IoC induction training, but only for self-generated, not for external sounds. These findings suggest that prior contextual belief information induced by an IoC affects later processing as reflected in the P2/P3a, possibly for the formation of agency judgments, while early processing reflecting motor-based predictions is not affected.

KEYWORDS

auditory ERP, EEG, illusion of control, sense of agency, sensory prediction

1 | INTRODUCTION

When processing sensory inputs, it is essential to distinguish those caused by our own actions (e.g., touching oneself) from those with an external cause (e.g., being touched by another agent). Self- and externally generated stimuli appear to be treated differently by our perceptual system. Sensory attenuation, that is a decreased perceptual intensity for sensory stimuli caused by our own actions compared to physically identical but externally generated stimuli, has been a common finding in different sensory modalities (Cardoso-Leite et al., 2010; Sato, 2008; Shergill et al., 2005). A related finding is the reduction of neuronal responses associated with processing self- versus externally generated sensory stimuli

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(Baess et al., 2011; Horváth, 2015; Hughes & Waszak, 2011), although a recent study suggested that these two phenomena might be based on different underlying processes (Palmer et al., 2016).

According to the classic interpretation, both phenomena can be explained by assuming internal forward models (Pickering & Clark, 2014; Reznik et al., 2014; Wolpert & Flanagan, 2001) that predict the sensory consequences of voluntary movements. This type of prediction is thought to be performed by the cerebellum and based on efference copies of commands sent by the supplementary motor cortex (Blakemore et al., 2001; Haggard & Whitford, 2004; Popa & Ebner, 2018; Reznik et al., 2015), which are available even before the initiation of a movement (Crapse & Sommer, 2008; Reznik et al., 2018; Vercillo et al., 2018; von Holst & Mittelstaedt, 1950). Sensory input occurring after movements could thus be compared immediately to the predicted input, with matches possibly resulting in altered subsequent neural processing and ultimately adjusted perception. In line with this notion, it has been shown that these phenomena depend on motor intention, not motor execution. Voss et al. (2006) reported sensory attenuation for somatosensory stimuli before the actual movement when transcranial magnetic stimulation (TMS) delayed its execution, while neuronal responses for auditory stimuli caused by involuntary movements that were generated with TMS over the primary motor cortex were not reduced (Timm et al., 2014).

In the auditory domain, which has been studied extensively in the last decades (Horváth, 2015), electroencephalography (EEG) recordings have consistently revealed that the processing of self- versus externally generated auditory stimuli is associated with amplitude reductions of the event-related potential (ERP) component N1 and (although findings are less consistent) of the P2/P3a (Baess et al., 2011; Ghio et al., 2018; Horváth, 2015; Horváth et al., 2012; Knolle et al., 2012; Lange, 2009, 2011; Schafer & Marcus, 1973; Timm et al., 2013, 2016). An increasing number of studies seem to suggest a functional dissociation between the early N1 and the later positive component(s). For example, cerebellar lesion patients showed no reduction of the N1 amplitude for self-generated sounds, but a reduction of P2 amplitudes similar to controls (Knolle et al., 2013). A possible interpretation is that only the early sensory processing as reflected by the N1 is modulated by cerebellar forward model predictions based on motor information. A similar dissociation can be found when comparing the processing of self-generated to cue external sounds. Even though self-generated and cued sounds are similarly predictable, the N1 for cued sounds is not attenuated compared to non-cued external sounds (Lange, 2011; Sowman et al., 2012), indicating that the process underlying the attenuation requires motor information. A P2 attenuation, moreover, was observed for cued external sounds (Sowman et al., 2012), again suggesting that a different, possibly higher order prediction mechanism is used at this stage, not critically depending on motor information.

Previous studies associated the (mis)matching of predicted and perceived sensory input with an internal interpretation of sensory input as self-generated (if it matches the prediction) or as externally generated (if there is a mismatch), suggesting a contribution to the subjective experience of agency, that is, of being responsible for the experienced sensory stimulation (Blakemore et al., 2000, 2002; Synofzik et al., 2013). For example, schizophrenic patients with altered feelings of agency, reflected in the typical symptoms of auditory hallucinations and passivity experiences, showed reduced sensory attenuation for self-produced sounds and forces (Blakemore et al., 2000, 2002; Shergill et al., 2005). Furthermore, diminished N1 amplitude reductions for self-relative to externally generated auditory stimuli was found in schizophrenic patients (Ford et al., 2007, 2013; Heinks-Maldonado et al., 2007), suggesting that impaired prediction mechanisms may play a role for deficits in the distinction between self- and externally generated stimuli and thus for the experience of agency. However, Ford et al. (2013) did not find a significant correlation between the deficient N1 reduction and schizophrenia symptoms, questioning the relationship between the N1 modulation and agency.

Some studies on healthy participants experimentally manipulated the sense of agency to examine whether and which ERP components are modulated by agency in the processing of self- or externally generated stimuli. Kühn et al. (2011) induced uncertainty about the authorship of self-produced sounds by varying their delay and pitch, while suggesting that some sounds may be generated by the experimenter. Agency ratings for each sound were collected, and no difference was found for the auditory N1 amplitude between trials with high and low agency ratings. The P3a, a component associated with unexpected stimuli (Herrmann & Knight, 2001), was, however, significantly reduced for sounds judged as self-generated. While amplitudes of the P2 were not analyzed, visual inspection suggests that it was not affected by agency. In a related study, Timm et al. (2016) successfully manipulated agency by presenting delayed or non-delayed tones when delayed tones were expected, which resulted in a high and low agency condition, respectively. In line with the findings of no agency effect on the N1 (Ford et al., 2013; Kühn et al., 2011), these authors found a comparable reduction of N1 amplitudes for self- versus externally generated sounds in both agency conditions. However, for the P2 an agency effect emerged: amplitude reductions for self-generated tones were less pronounced in the low agency condition. Overall, the emerging pattern in the findings suggests that distinct prediction mechanisms are reflected in the early and late ERP components for the processing of self-generated stimuli. The N1 seems to reflect simple predictions directly linked to motor actions and appears unaffected by context-dependent variations in agency, whereas the later positive components (P2 or P3a) appear to reflect prediction mechanisms sensitive to top-down influences such as context-dependent modulations of subjective agency.

It has been shown that agency over the production of a sound is also modulated by the predictability of its occurrence, as reducing the probability of sounds being played following button presses lowered subjective agency for those sounds that did occur, as revealed by an implicit behavioral measure (Moore & Haggard, 2008; Moore et al., 2009). Furthermore, agency is sensitive to the contingency of action and outcome (Moore et al., 2009). Contingency is commonly calculated as the difference between the probability of an outcome given a potential cause, for example, a movement, and the probability of the outcome in the absence of the potential cause (Allan, 1980; Jenkins & Ward, 1965). If the outcome (e.g., a tone) occurs with the same probability after an action (e.g., button press) and without it, the difference is zero and the relation is thus non-contingent. In this context, it is important to note that contingency in non-contingent action-outcome paradigms is generally overestimated, an effect that is known as the illusion of control (IoC) (Langer, 1975). Research has shown that increasing the probability of the outcome in non-contingent paradigms increases the level of perceived control over the outcome, thereby enhancing the IoC and thus the perceived contingency (Blanco et al., 2013; Jenkins & Ward, 1965; Matute et al., 2015; Studer et al., 2020; Thompson et al., 2007).

In the present study, we combined research on the IoC and on the processing of self-generated stimuli. More specifically, we examined whether differences in the perceived personal control affect subsequent processing of self-generated sounds. To manipulate perceived control, we used a new version of a classic two-button choice task (Jenkins & Ward, 1965), in which participants chose a button in each trial in order to produce a desired auditory outcome stimulus and the probability of the desired auditory outcome was manipulated to induce a stronger or weaker IoC. We recently showed that induced levels of illusory control affected subsequent behavioral persistence in two different motivationally challenging situations (Studer et al., 2020). This suggests that IoC effects can extend beyond the conditions in which IOC was induced. In the current study, we aimed to test if induced IoC over generating a specific sound could also affect auditory processing of physically identical self-generated sounds in a subsequent structurally different task, namely in the self-generation paradigm. In analogy to findings on agency manipulations (Kühn et al., 2011; Timm et al., 2016), we expected no effect of the IoC on the N1 amplitude reduction for self- compared to externally generated sounds. Instead, we expected an effect of the IoC on later processing in the P2 time window. In particular, amplitude reductions for self-generated tones were expected to be larger for higher levels of IoC, since the P2 seems to be sensitive to top-down influences like expectancy and agency (Kühn et al., 2011; Sowman et al., 2012; Timm et al., 2016).

2 | METHOD

2.1 | Participants

Forty participants took part in the experiment (33 women, M_{Age} = 25.4 years, SD_{Age} = 3.5 years) and received either course credit or monetary compensation. Normal or corrected-to-normal vision and normal hearing (according to self-report) were requirements for participation. The experiment was approved by the Ethics Committee of the Faculty of Mathematics and Natural Sciences at Heinrich Heine University Düsseldorf, Germany, and written informed consent was given by all participants.

2.2 | Procedure

To examine the effect of IoC on the processing of self- versus externally generated sounds, we set up a within-subject design that included two experimental blocks, each consisting of two tasks. In both blocks, participants were first exposed to a two-button choice task, designed to induce either a high or low level of perceived control over the production of desired sound (as opposed to an undesired sound), over which they actually exercised no control (from now on referred to as the IoC task). We aimed to achieve this by varying the base probability P(O) for the desired auditory outcome regardless of the button choice (see below). With this manipulation we wanted to modulate the processing of self- (Act-sounds) versus externally generated sounds (Ext-sounds) in a subsequent, so-called self-generation paradigm (Horváth, 2015), which was conducted as a second task in each experimental block. Indeed, our main interest in this study was to examine the effect of the IoC, as induced by the IoC task, on the neuronal processing of Act-sounds versus Ext-sounds in the self-generation paradigm, assessed by means of EEG. To distinguish this effect from a possibly carried over identity association between action and sound (Hughes et al., 2013), button presses were performed on different buttons in the two tasks. As we employed a within-subject design, the self-generation paradigm was performed twice, once after the IoC task with high P(O) (from now on the sequence of these two tasks is referred to as high P(O) block), and once after the IoC task with low P(O) (referred to as low P(O) block). As we wanted to test if the P(O) in the IoC task could affect neuronal processing of sounds in the subsequent task, the self-generation paradigm in the high P(O) block will be referred to as high P(O) condition, whereas the self-generation paradigm in the low P(O) block will be referred to as low P(O) condition, although the self-generation paradigm itself was identical in both blocks. Whether participants started with the low or high P(O) block was counterbalanced across participants (see Figure 1 for a schematic representation).

Stimulus presentation and response recording were controlled by Presentation software (Version 17.0, Neurobehavioral Systems, Inc., Berkeley, CA, www.neurobs.com) on a Windows 10 PC. Sound was delivered through an onboard soundcard (Realtek ALC887-VD) in DirectX Software mode and Sennheiser HD 202 headphones. Button presses were registered with a Cedrus RB-740 response pad (www.cedrus.com) featuring seven response buttons oriented in a straight horizontal line. The leftmost and rightmost buttons were used in the IoC induction task, while the middle button was pressed during the self-generation paradigm. This procedure was applied in order to avoid carryover effects of specific action-outcome associations. Ratings in the IoC task and Act-sound condition (see below) were given with a regular keyboard.

2.2.1 | IoC induction

Our IoC task was a variant of the classic two-button choice task by Jenkins and Ward (1965). In this task, participants were asked to try to elicit a desired auditory outcome by means of button presses. Participants chose between two buttons on every trial, but the outcome (i.e., desired vs. undesired sound) in each trial did not depend on the action that was performed (Allan, 1980; Matute et al., 2015). Instead, the P(O) for the desired sound was fixed by predetermining the outcome of every trial before the start of the task, and the P(O) varied between conditions in order to elicit a high or low IoC. Specifically, in the IoC task with high P(O), the desired sound was presented in 70% of the trials (total number of trials = 100), while for the remaining 30% of the trials an undesired sound was presented, irrespective of what button was pressed in the respective trial. In turn, in the IoC task with low P(O), the desired sound was presented in 30% of the trials (total number of trials = 100) and the undesired sound in 70% of the trials, again regardless of which button was pressed.

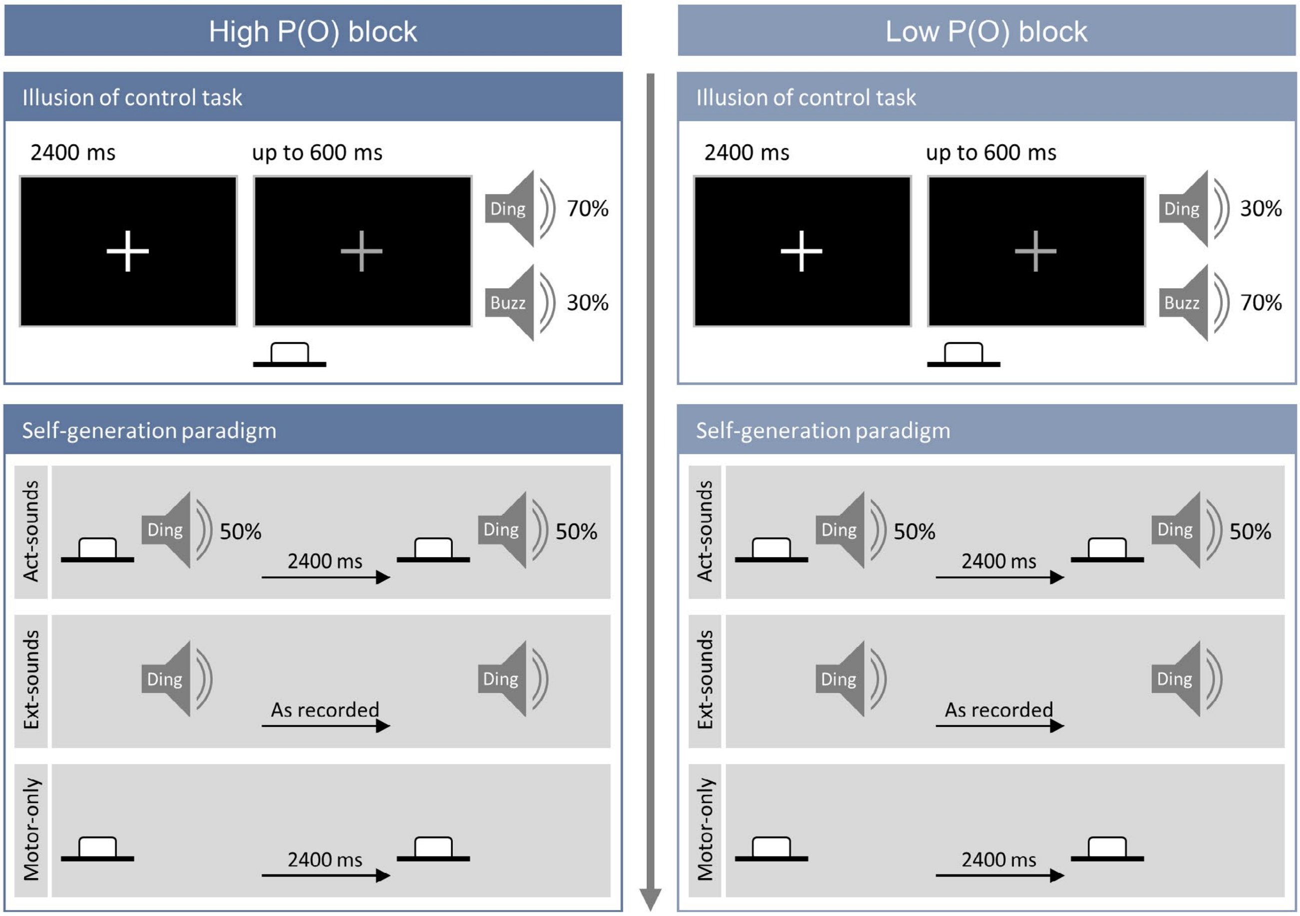

FIGURE 1 Experimental sequence for the high and low probability block (High P(O) block on the left and Low P(O) block on the right). Task order is indicated by the arrow, ending with the identical self-generation paradigm in both blocks

Each trial started with a white fixation cross on a black background. After 2,400 ms the fixation cross color switched to grey for 600 ms. Participants were asked to press one of the two available buttons (i.e., the leftmost or rightmost button on the response pad) as soon as the color of the fixation cross changed from white to grey in order to produce a desired sound that was introduced in the instruction as a positive sound ("ding.wav," distributed with Windows XP, 100 ms duration). The rhythm of one button press every 2,400 ms was introduced in order to train participants to this rhythm for the subsequent self-generation paradigm, which required regular self-paced button presses (see Ghio et al., 2018; Knolle et al., 2013). Each button press was followed either by the desired sound (70% and 30% of the trials in the IoC task with high and low P(O), respectively) or by an undesired sound (introduced in the instructions as a negative sound, namely a synthetic buzzer sound, 100 ms duration), irrespective of what button was pressed in the trial. The sounds were presented 50 ms after button press onset (see Ghio et al., 2018). As a further motivation to try to elicit the desired sound, each occurrence of the sound during the IoC task was associated with a monetary reward of 0.20 €, whereas each undesired sound was associated with a monetary loss of 0.05 €. Button presses occurring during the white fixation cross and thus outside of the required rhythm were penalized with a loss of 0.20 €. On average, every 15 trials (with a random variance of ±5 trials) participants were asked "*How much control did you have over the generation of the positive tone?*" and prompted to rate their level of control on a visual analog scale ranging from 0 (*NO control - the appearance of the positive sound had nothing to do with your button press*) to 100 (*COMPLETE control – the appearance of the positive sound was entirely determined by your button press*) presented on the screen. A medium level of control was described as "*MEDIUM control - your button press had an influence on the appearance of the positive sound. You did however not fully control it*."

2.2.2 | Self-generation paradigm

The self-generation paradigm comprised three experimental conditions in a fixed order, which were presented in separate sub-blocks and did not differ between the high and low P(O) condition. Throughout all conditions, a white fixation cross was displayed.

Act-sound condition

Subjects were instructed to press the middle button on the response pad (thus, a button different from those used in the IoC task) with their right index finger in the same rhythm that was learned in the IoC task (i.e., every 2,400 ms ca.). Different from the standard self-generation paradigm in which each button press generates a sound (Horváth, 2015), button presses in our paradigm (n = 200) were followed by a sound only in 50% of the trials (n = 100 for the number of sounds). This variation was adopted in order to create uncertainty concerning the association between button presses and sounds and to prevent the preceding IoC induction from decaying during the beginning of the task. Importantly, the sound used in the self-generation paradigm was identical to the desired sound in the IoC task, while the undesired sound was never presented. On average, every 20 trials (with a random variance of ±5 trials) participants were prompted to rate their level of control over the production of the sound, applying the same scale used in the IoC task (see above). After each rating, they also received feedback concerning the length of their button press interval in the previous 20 (±5) trials. If 25% of these intervals deviated more than 600 ms from the required duration of 2,400 ms in one direction, participants were asked to react faster or slower, respectively. Otherwise, they were encouraged to keep their current rhythm.

Ext-sound condition

Subjects were presented with the playback of all the 100 sounds generated in the previous Act-sound condition and instructed to listen to them carefully without performing any action.

Motor-only condition

To control for the motor demand present in the Act-sound condition (see below for details), participants were asked to press the button in the same rhythm applied in the Act-sound condition (i.e., every 2,400 ms ca.). Crucially, no sounds were presented.

2.3 | EEG Data acquisition and preprocessing

EEG data were continuously recorded at 1,000 Hz with BrainVision Recorder software (1.20.0506, Brain Products, GmbH, Germany). Twenty-eight Ag/AgCl passive ring electrodes connected to a BrainAmp amplifier were positioned on the scalp via an elastic cap (EasyCap). According to the international 10–20 System, electrodes were positioned at F7, F3, Fz, F4, F8, FT7, FC3, FCz, FC4, FT8, T7, C3, Cz, C4, T8, CP3, CPz, CP4, P7, P3, Pz, P4, P8, PO7, PO3, POz, PO4, and PO8. The recorded signal was referenced to linked mastoids, and the ground electrode was placed at AFz. Electrooculogram data were recorded at F9 and F10 for horizontal eye movements. To register vertical eye movements, one electrode was positioned below the right eye, aligning with a second electrode at Fp2. Impedances were kept below 5 kΩ.

Raw EEG data recorded during the self-generation paradigm in the high and low P(O) condition were analyzed with

Brain Vision Analyzer 2.2 (Brain Products) and MATLAB (R2018a, The MathWorks, Inc., Natick, MA). After a global direct current de-trend, a Butterworth zero-phase filter (low cutoff: 0.3 Hz, 12 dB/oct; high cutoff: 30 Hz, 12 dB/oct) and a notch filter (50 Hz) were applied. An independent component analysis (steps = 512, infomax restricted biased) was employed to identify components reflecting blinks, horizontal and vertical eye movements and remove them before a subsequent inverted ICA.

ERP segments were time-locked to the onsets of the sounds in the Act-sound and the Ext-sound condition and had a duration of 600 ms (including a 150 ms pre-sound period). As the interval between button press onset and tone onset was 50 ms (see above) the segment lasted from 100 ms before to 500 ms after the button press onset in the Act-sound condition. For the Motor-only condition, corresponding segments were created from −100 to 500 ms relative to button press onset.

Successive button presses and sounds appearing in an interval smaller than 1 s were excluded from further analyses. Epochs were baseline corrected by the mean amplitude of the first 100 ms of the interval, that is, from 150 ms to 50 ms before sound onset in the Act- and Ext-sound conditions and from 100 ms to 0 ms before button press onset in the Motor-only condition. Segments containing artifacts were detected and rejected using the automatic algorithm provided by BrainVision Analyzer (maximal allowed voltage step = 50 μV/ms, maximal allowed difference of values within 100-ms intervals = 100 μV, maximal/minimal allowed amplitude = ±100 μV, lowest activity of 0.5 μV within 100 ms intervals). Remaining segments were averaged separately for the Act-sound, Ext-sound, and Motor-only conditions and in the high and low P(O) conditions. In order to control for motor activity in the Act-sound condition (see Horváth, 2015), we then subtracted the average ERP of the Motor-only condition from the average Act-sound ERP. From now on the Act-sound condition will refer to the ERPs yielded by the ERP subtraction procedure. As differing action frequencies can cause processing differences both related to the actions and the elicited sounds, the average time interval between button presses was compared in a 2x2 repeated measure ANOVA with the factors Condition (Act-sound, Motor-only) and P(O) (low, high). Although the main effect of Condition was significant, $F(1, 28) = 5.11$, $p = .026$, $\eta_p^2 = .044$, with longer time intervals in the Motor-only (M = 3,088 ms, SD = 929) than in the Act-sound condition (M = 2,731 ms, SD = 546), we still consider the ERPs in the Motor-only condition as an appropriate control for the motor-related ERPs in the Act-sound condition, as in absolute terms the difference was small and the intervals were long enough for the motor ERPs to return to baseline. Importantly, the interaction, $F(1, 28) = 0.35$, $p = .556$, $\eta_p^2 = .003$, and the main effect for P(O), $F(1, 28) = 0.45$, $p = .503$, $\eta_p^2 = .004$, were not significant, indicating that action- and sound-related ERPs could not be affected by P(O)-dependent differences in the timing of actions and/or sounds. Concerning the inter-response-intervals (IRIs) after button presses that did (M = 2,688 ms, SD = 569 ms) and did not elicit sounds (M = 2,666 ms, SD = 538 ms), in the Act-sound condition no significant difference was found, as revealed by a paired sample t test, $t(28) = 0.294$, $p = .771$, $d = .06$. We did, however, see large interindividual differences in the (dis)similarity of these intervals (see section 2.4).

Finally, the mean amplitudes for the two ERP components of interest, N1 and P2, were extracted for the Act-sound and Ext-sound conditions, separately for the high and low P(O) conditions. To determine time windows and electrode positions for the analysis of these components, we created two grand averages, one for the Act- and one for Ext-sounds, across P(O) conditions. We avoided an overall grand average across sound types, as the P2 showed a notable latency difference between Act- and Ext-sounds (see supplementary materials). Based on the topographical maps of the two grand average N1 peaks, we determined FCz and Cz as appropriate electrode positions for our analysis, focusing on the midline electrode sites as previously suggested (Knolle et al., 2013; Timm et al., 2016). For the later positive component, mappings indicated highest activity at Cz and CPz for Act-sounds and at FCz and Cz for the Ext-sounds. We, therefore, included FCz, Cz, and CPz in our P2 analysis. N1 peak latencies were extracted from the two grand averages and then averaged for both electrodes. As the latencies for the two sound type conditions were very similar (Act-sounds: 84 ms; Ext-sounds: 92 ms) the mean signal in one N1 time window from 68 ms to 108 ms was considered to appropriately reflect N1 amplitude for both conditions. For the P2, the latencies in the two conditions clearly differed (Act-sounds: 255 ms; Ext-sounds: 180 ms). Therefore, we defined separate time windows for the two sound type conditions, from 235 ms to 275 ms for Act-sounds and from 160 ms to 200 ms for Ext-sounds. Mean amplitudes were measured in these time windows for all conditions and the respective electrodes.

2.4 | Data analysis

From the sample of 40 participants, we excluded one participant for missing data at the Cz electrode and one for excessive artifacts and a consequent loss of more than 50% of the ERP segments for the analysis. Three participants were determined as outliers due to the length of their IRIs in the Act-sound condition or Motor-only condition and one due to an enlarged difference between IRIs following button presses that did or did not elicit sounds, as these four participants each showed a deviation of more than 2.5 SDs from the sample mean. Furthermore, we excluded five participants for rating their level of control in the high P(O) condition lower than in the low P(O) condition (namely their rating difference was <0, see below for an explanation about how this indicates that the intended IoC induction was unsuccessful). The data of the remaining 29 participants (22 women, 26 right-handed, $M_{\text{Age}} = 25.2$ years, $SD_{\text{Age}} = 3.2$ years) were then entered into the statistical analyses for EEG and behavioral data. All analyses were conducted in R (version 3.6.3) using RStudio (version 1.3.959).

2.4.1 | Behavioral data

To determine whether the IoC task with the high P(O) induced a stronger IoC than the IoC task with low P(O), average control ratings in the two IoC task versions were calculated and compared by means of paired *t* tests. Furthermore, we calculated the difference in the control ratings in the IoC task with high and low P(O) for each participant, which will be referred to as the rating difference (RD) in the following. Positive values indicate higher perceived control in the IoC task with high P(O), as intended, whereas negative values indicate the opposite pattern. To exclude order effects, RD values were compared via Welch *t* test between participants who started with the high ($n = 17$) or low ($n = 12$) P(O) condition. All analyses were performed with the default R stats package, Cohen's *d* values for *t* tests were calculated with the R package lsr (version 0.5). An α level of .05 was considered as statistically significant. For completeness, identical analyses on the control ratings in the self-generation paradigm are reported in the supplementary materials.

2.4.2 | EEG Data

Of central importance for the present study was the relationship between ERP measures of auditory processing and the subjective control ratings in the IoC task with high and low P(O), since they reflect the success of the intended IoC induction. The large interindividual variability for the difference measure (RD), from 0.6% to 49% (see Figure 2 for a histogram), suggested that the high and low P(O) IoC task induced different levels of perceived control in each participant. Consequently, the effect on the processing of the Act- and Ext-sounds likely also varied between participants. We thus aimed to include the continuous variable RD in the statistical model. To achieve this, we analyzed the data by means of a linear mixed-effects analyses (LME), in which both categorical and continuous independent variables can be included (Baayen et al., 2008).

Several separate LME analyses were performed using the lme4 package (version 1.1 23). The N1 analysis was conducted on the mean amplitudes in the N1 time window (see above). P2 was analyzed using the mean amplitudes in the Act-sound P2 peak time window for Act-sounds and in the Ext-sound P2 peak time window for Ext-sounds. See supplementary materials for an alternative analysis that directly compares N1 and P2 mean amplitudes in one model. To explore if the ERPs of the Act-sound condition already differed between P(O) conditions in the earlier Ext-sound P2 peak time window, as suggested by visual inspection, an additional analysis included the mean amplitudes in this time window for all conditions.

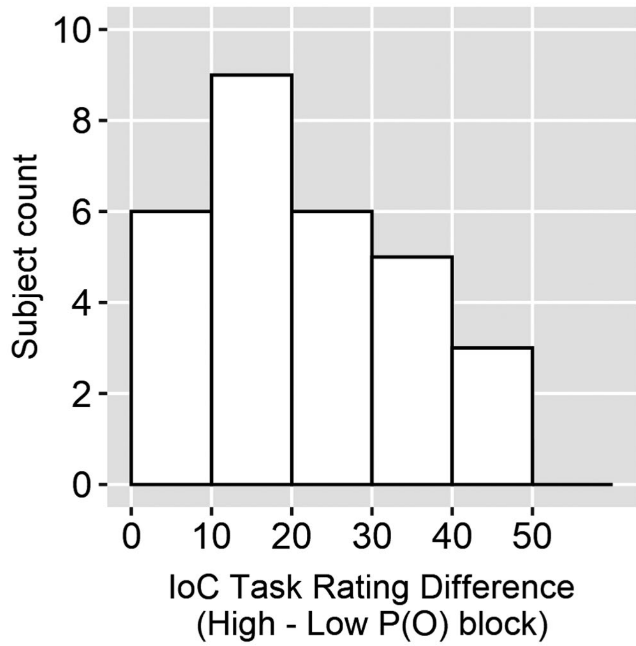

FIGURE 2 Histogram of participants in the final sample ($n = 29$) according to their differences between the level of control ratings in the IoC task of the High and Low P(O) block. From the sample of 40 participants, five participants were excluded for IoC task rating differences below zero (see section 2.4), in addition to six participants excluded as outliers or due to technical reasons

For each analysis, we created a model comprising the fixed-effect predictors Sound type, P(O) and RD. RD was mean-centered and entered into the model as a continuous fixed-effect predictor. The categorical predictors Sound Type (0.5 = Act-sounds, −0.5 = Ext-sounds) and P(O) (0.5 = high, −0.5 = low) were simple coded. Interactions between all three predictors were modeled, and random intercepts and slopes (for Sound type and P[O]) by participants were modeled as random effects. As we included the data of several electrodes in each model (see above), we modeled a random intercept for the electrode as a random effect nested in the random effect Participant (see supplementary materials for the R model syntax). We used the restricted maximum likelihood approach for model estimation and assessed significance with the R package lmerTest 3.0-1 (Kuznetsova et al., 2017) and its built-in Satterthwaite approximation for the degrees of freedom. This is in line with suggestions by

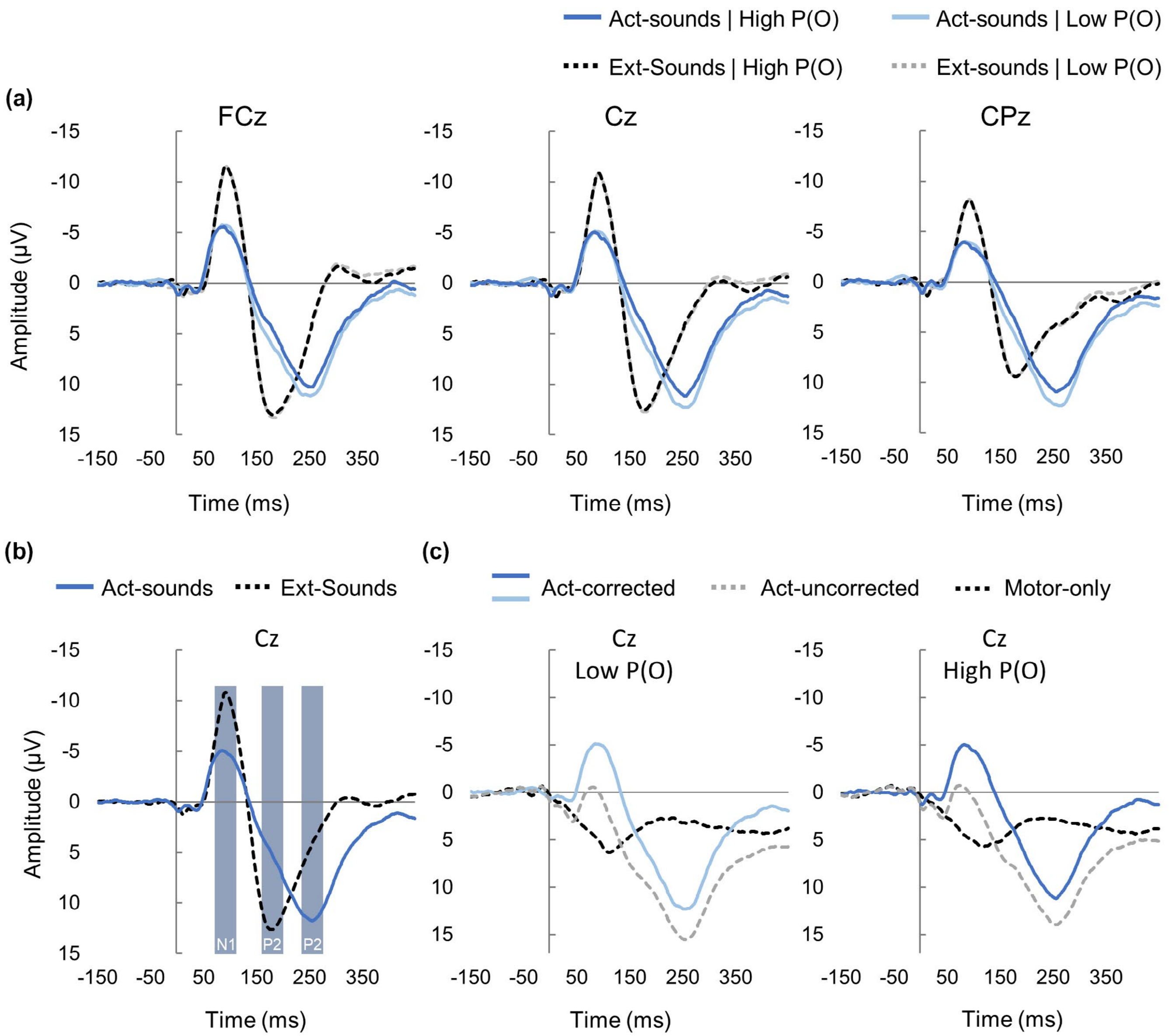

FIGURE 3 (a) Grand average ERPs for all analyzed electrode sites in the Act- and Ext-sound conditions and in the low and high P(O) conditions, with the y-axis intersecting at the start of the sound event. (b) Grand average ERPs at Cz for the Act-sound and Ext-sound condition across P(O) conditions, used to determine the shown time windows (68–108 ms, 160–200 ms, 235–275 ms) for mean amplitude extraction (see section 2.3). (c) Grand average ERPs at Cz showing the uncorrected and corrected Act-sound condition, as well as the Motor-only condition, separately for the low and high P(O) condition

Luke (2017), reporting acceptable Type I error rates, largely independent of sample size, compared to the common likelihood ratio tests. After building our statistical models for the EEG data analysis, we investigated whether any participants emerged as an influential data point by applying the R package influence.ME (Nieuwenhuis et al., 2012). As an exclusion criterion, we defined that participants had to emerge as an influential data point in both the N1 and P2 models in order to be excluded, which was not the case for any of our participants. After performing the LME analyses, however, we additionally investigated the impact of each detected influential data point in one model on the results of that model, by the separate exclusion of each outlier and re-analysis of the corresponding model. We found neither loss of significance for the reported effects, nor a significant new effect in any of the single-participant-exclusion models.

Simple effects analyses for the resolution of significant interactions were conducted by dummy coding the categorical factors' reference condition to 0 and shifting the center of the continuous factor RD by one standard deviation up or down in two separate analyses (Aiken et al., 1991; Liu et al., 2017). We will refer to the simple effects at these recentered values as being "low" and "high" values of RD. Marginal means (for plotting) were calculated with the R package ggeffect (version 0.16.0). An α level of .05 was considered statistically significant. Significant effects of the predictor RD are only reported in interactions with P(O).

3 | RESULTS

3.1 | Behavioral data

Subjective control ratings in the IoC task were significantly higher in the high P(O) block (M = 60.3%, SD = 13.1%) than in the low P(O) block (M = 39.1%, SD = 16.3%, $t(28) = 8.50$, $p < .001$, $d = 1.58$). Figure 2 shows a histogram of RD values. No significant differences were found when comparing RD values in the IOC task between participants who started with the high P(O) condition and participants who started with the low P(O) condition, $t(24.92) = -1.46$, $p = .157$, $d = .55$.

3.2 | EEG data

Figure 3a shows grand average ERPs for Cz, FCz, and CPz in the Act- and Ext-sound conditions and in the low and high P(O) conditions. Figure 3b shows overall grand averages for the Act- and Ext-sound condition across P(O) conditions at Cz, which was used for determining the different P2 time windows for these conditions (see Methods section). In Figure 3c, the subtraction procedure for the correction of the Act- sound ERPs is illustrated. Figure 4 shows topographical maps of N1 and P2 amplitudes in all conditions and Figure 5 shows N1 and P2 mean amplitudes in all conditions as a function of the RD values. Table 1 contains descriptive statistics for all analyzed components.

3.2.1 | N1 component

Model fit statistics for the N1 amplitude revealed a significant main effect of Sound type, $F(1, 27) = 25.75$, $p < .001$, and parameter estimates suggested significantly smaller amplitudes for Act-sounds compared to Ext-sounds ($b = 4.25$, $p < .001$, see the left scatterplot in Figure 5). No further significant main or interaction effects were found (all $ps > .114$).

3.2.2 | P2 component

First, we performed the analysis on the P2 mean amplitude by separate time windows for the Act-sound and Ext-sound condition as the P2 amplitude showed a noticeable difference in their latencies between the two conditions (for an analysis of the latencies see supplementary materials). The analysis of the amplitudes revealed no significant main effect of Sound type, $F(1, 27) = 0.01$, $p = .934$, but a significant Sound type by P(O) condition interaction, $F(1, 201) = 9.02$, $p = .003$. A follow-up simple effects analysis showed that for Act-sounds amplitudes in the high P(O) condition were significantly lower than in the low P(O) condition, $F(1, 35.12) = 5.22$, $p = .028$, $b = -1.32$, but no effect of P(O) emerged for Ext-sounds, $F(1, 35.12) = 0.03$, $p = .869$. Furthermore, we found a significant Sound type by P(O) condition by RD interaction, $F(1, 201) = 6.91$, $p = .009$ (see the middle scatterplot in Figure 5 and for further visualization of this interaction, Figure 6). Resolving the three-way interaction with a simple slope analysis showed that the interaction between Sound type and P(O) condition was significant for high RD values, $F(1, 201) = 15.86$, $p < .001$, but not for low RD values, $F(1, 201) = 0.07$, $p = .793$ (see Figure 6). In a follow-up simple effects analysis to resolve this interaction, a trend

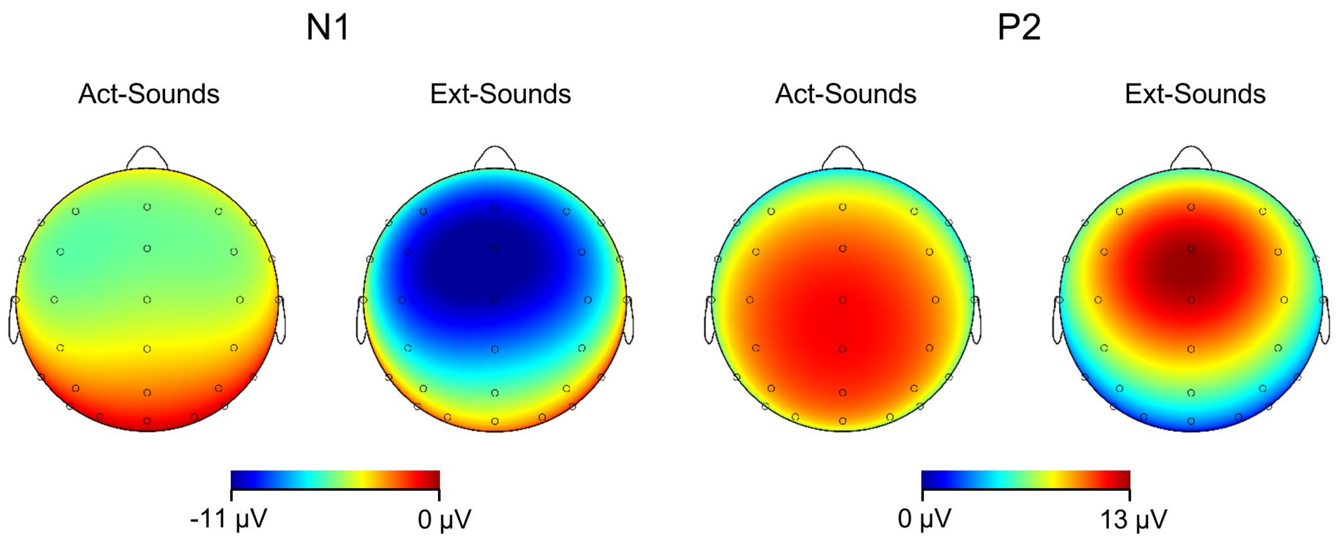

FIGURE 4 Topographical maps showing scalp potentials for the N1 and P2 at grand-average peak latencies separately for the Act-sound condition and Ext-sound condition (pooled across P(O) conditions)

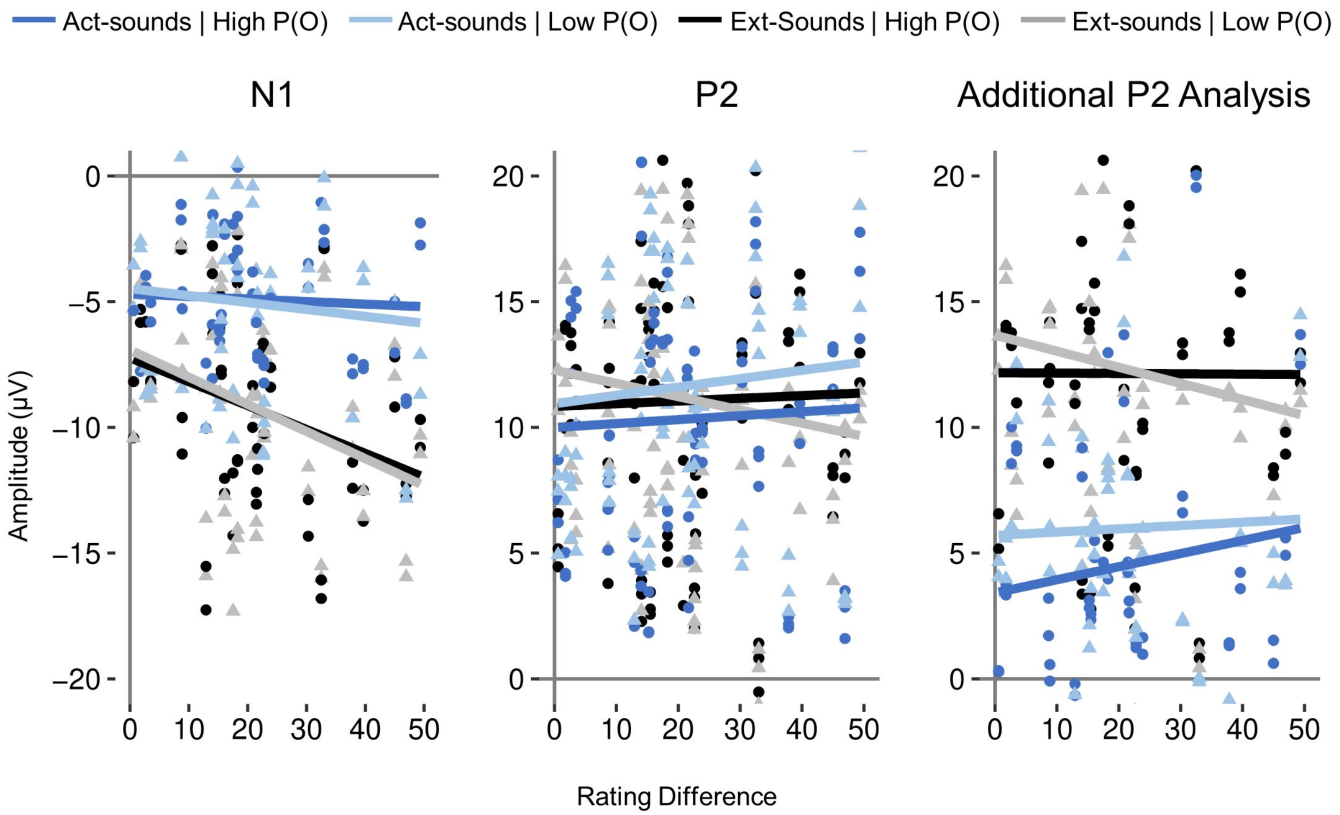

FIGURE 5 Scatter plots for the extracted N1 and P2 amplitudes as a function of participants' rating difference values. Data points and regression lines are shown separately for Act- and Ext-sounds in the low and high P(O) conditions. The plots are restricted to the y-axis segment from 0 μV to −20 μV for the N1 data, and from 0 μV to 20 μV for the P2 data to facilitate visibility of the regression lines, which are still based on the entire data

TABLE 1 Descriptive statistics of data used in the analyses

		Act-sounds		Ext-sounds		Act-sounds		Ext-sounds	
		High P(O)		High P(O)		Low P(O)		Low P(O)	
	Electrode	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
N1 analysis	FCz	−5.18	2.54	−9.55	4.01	−5.37	4.33	−9.49	4.25
	Cz	−4.63	2.66	−8.95	3.77	−4.76	4.32	−8.94	4.07
	CPz	−3.60	2.61	−6.83	3.04	−3.74	3.64	−6.89	3.43
P2 analysis	FCz	9.79	5.61	12.40	6.42	10.87	5.80	12.59	6.69
	Cz	10.69	5.72	11.89	5.99	12.06	6.09	12.03	6.43
	CPz	10.51	5.23	8.90	4.87	12.01	5.82	8.85	4.95
Additional P2 analysis	FCz	4.58	5.30	12.40	6.42	6.01	5.48	12.59	6.69
	Cz	4.47	5.22	11.89	5.99	5.95	5.32	12.03	6.43
	CPz	4.06	4.55	8.90	4.87	5.40	4.78	8.85	4.95

Note: Estimated means and standard deviations for the data used in the N1, P2, and additional P2 analysis (using only data from the Ext-sound P2 peak time window) separately for each electrode and the levels of the factors Sound type and P(O).

emerged for participants with higher values of RD concerning the effect of P(O) for Act-sounds, $F(1, 35.12) = 3.60$, $p = .066$, while the effect was not significant for Ext-sounds, $F(1, 35.12) = 0.83$, $p = .369$. According to parameter estimates, amplitudes for Act-sounds were reduced in the high compared to the low P(O) condition for participants with high RD values ($b = -1.55$, $p = .066$). The other main effects and interactions did not reach significance (all *p*s > .201).

Second, we report an additional analysis of the mean amplitudes for both conditions in the Ext-sound P2 peak time

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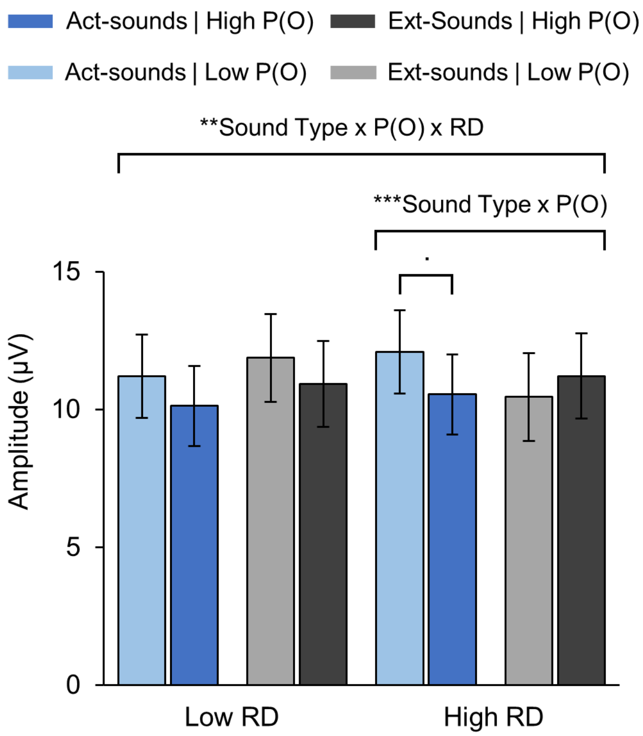

FIGURE 6 Bar plot for the marginal means of the P2 model with separate bars for Act- and Ext-sounds in the low and high P(O) conditions at either low (−1 *SD*) or high (+1 *SD*) values of the continuous, mean-centered factor RD. Error bars show standard errors. Significances yielded by the Sound Type by P(O) by RD interaction and the analyses of the simple effects conducted to resolve it are indicated by . $p < .1$, ** $p < .01$., *** $p < .001$

window. The model fit revealed a significant main effect of Sound type, $F(1, 27) = 33.88$, $p < .001$, with smaller amplitudes for Act-sounds compared to Ext-sounds ($b = -6.97$, $p < .001$). The Sound type by P(O) condition interaction was also significant, $F(1, 114) = 15.56$, $p < .001$ (see the right scatterplot in Figure 5). A simple slope analysis to resolve the interaction revealed significantly reduced amplitudes in the high P(O) compared to the low P(O) condition only for Act-sounds, $F(1, 34.7) = 9.54$, $p = .004$, $b = -1.46$, but not for Ext-sounds, $F(1, 34.7) = 0.13$, $p = .724$. None of the other main effects or interactions were significant (all *ps* > .077).

4 | DISCUSSION

In this study, we investigated the influence of the IoC on reductions of neuronal responses to self-generated compared to external sounds. In a within-subject design, we presented participants with two versions of a classic two-button choice task (Jenkins & Ward, 1965) in order to induce either a strong or weak IoC. Explicit ratings of perceived control in the high P(O) and the low P(O) confirmed that our IoC induction worked. Each IoC induction was followed by the same self-generation paradigm, in which participants performed regular button presses in one condition, with 50% of the button presses eliciting a sound, and listened to externally generated sounds in another condition. ERPs time-locked to sound onset were measured during this self-generation paradigm. For the N1 component, an amplitude reduction was found for Act-sounds relative to Ext-sounds, without modulation by IoC. P2 amplitudes were reduced under high versus low IoC, but only for Act-sounds and not for Ext-sounds. Additionally, the strength of IoC induction (measured as the difference in control ratings between the two IoC conditions) modulated the P2 reduction for Act-sounds. The results of the present study thus support our hypothesis that different levels of IoC would affect the later stages of the processing of self-generated sounds.

4.1 | Dissociation between early and late processing stages for self-generated sounds

In the original concept of forward models it has been proposed that one function of the comparison of their predictions with sensory input is to determine if stimuli are self-generated or not (Wolpert & Flanagan, 2001), finally resulting in agency attributions (Picard & Friston, 2014). Research on the reduced N1 amplitude for self-generated tones, which has been linked to forward model predictions, seem to support this assumption. For example, the typical symptoms in schizophrenic patients like passivity experiences and auditory hallucinations have been interpreted as misattributions of agency, resulting from impaired efference copies and consequent failures of matching predicted and experienced sensory input (Feinberg & Guazzelli, 1999; Spering et al., 2013; Swiney & Sousa, 2014; Synofzik et al., 2010). Indeed, diminished auditory N1 reductions were found in schizophrenia patients for sounds elicited by button presses (Ford et al., 2013) as well as for speech (Ford et al., 2007; Perez et al., 2012) compared to externally generated stimuli. Importantly, deficient auditory N1 reductions during an active speech in schizophrenia were found to correlate with errors in judging the source of the voice as one's own (Heinks-Maldonado et al., 2007), but mixed results have been reported for correlations of N1 reductions and schizophrenic symptom severity (Ford et al., 2007, 2013).

Moreover, our result pattern adds to evidence gained in previous studies that N1 reductions are not directly related to the judgment of agency (Kühn et al., 2011; Timm et al., 2016; Weller et al., 2017). Kühn et al. (2011), for example, reported comparable N1 reductions for self-generated sounds which were explicitly rated as self- or externally generated, and Timm et al. (2016) found unaltered N1 reductions in a condition with reduced agency. Corroborating this evidence, our manipulation of perceived control over sound production, which probably affected agency via effects on perceived contingency (Thompson et al., 2007), did not modulate the N1 amplitude. These results seem to suggest that the mere detection of a match between sensory input and motor-information-related predictions, which likely leads to the N1 reduction, is not sufficient for the formation of agency attributions. However, no firm conclusions can be drawn from negative findings, and further hints for interpreting the early component can come by considering it in relation to the later component(s).

Most previous studies on auditory ERPs for self-generated sounds have only distinguished between N1 and P2. The reported P2, however, appeared in different time windows (Horváth et al., 2012; Knolle et al., 2013; Sowman et al., 2012; Timm et al., 2014; Weller et al., 2017), and some did not exclude the possibility that another component, an early P3a (Baess et al., 2011; Ghio et al., 2018; Polich, 2007), contributes to stimulus processing in this paradigm. Furthermore, P2/3a reductions, unlike N1 reductions, were consistently reported also in paradigms and conditions in which predictions based on a forward model played no or only a minor role. For example, intact P2/3a reductions, but diminished N1 reductions, were found in healthy participants in the absence of own actions, for example, for sounds that were visually cued (Sowman et al., 2012), or predictable due to a button press by an observed person (Ghio et al., 2018). Likewise, cerebellar lesion patients with potentially impaired forward model predictions showed an intact P2 reduction, but no N1 reduction for self-generated versus external sounds. These findings indicate that the N1 and the P2/P3a might be functionally dissociated. Considering that both the P2 (Crowley & Colrain, 2004) and the P3a (Polich, 2007) are sensitive to the (un)expectedness of stimuli in oddball paradigms, these findings might suggest that both later components reflect higher level sensory prediction mechanisms that do not, or at least not exclusively, rely on the predictions of forward models.

4.2 | Agency in the early and late processing stages for self-generated sounds

It is interesting to note that Synofzik et al. (2008) conceptually distinguished between an automatic, intuitive feeling of agency about our own authorship, and a conscious judgment about which agent in the environment acted (Synofzik et al., 2008). According to this dual step account, the feeling of agency does not lead to an actual attribution of agency to an agent, but is a purely subjective experience, based on action-related authorship indicators, probably based on a comparison between forward model predictions and sensory feedback. The neural correlates of such a process could thus be reflected in the N1 component. The judgment of agency, moreover, is based on further processing of this feeling by integrating contextual cues and belief states to determine the most likely responsible agent. Evidence for the notion that the P2/3a components reflect this judgment of agency was reported in several studies in which agency was kept ambiguous by varying the timing or quality of a self-generated sound stimulus, requiring a postdictive agency judgment. Kühn et al. (2011) found that P3a reductions in a self-generation paradigm were less pronounced for sounds that were rated as externally generated compared to those that were rated as self-generated. Timm et al. (2016) showed that the magnitude of the P2 reduction in a condition with reduced agency was correlated with the proportion of trials in which no agency was perceived. P2 reductions were also found for sounds generated by observed actions (Ghio et al., 2020), indicating that agency attribution to another actor might be possible. The framework of optimal cue integration (Synofzik et al., 2013) extends the concept of the judgment of agency and proposes that predictive and postdictive sensorimotor and cognitive information are continuously integrated to form agency judgments. Overall, our results concerning the P2/3a can also be interpreted according to this framework, as the prior belief about high action-effect contingencies, which increases the perceived level of control (Thompson et al., 2007) and the agency experience (Moore et al., 2009), resulted in lower P2/3a amplitudes for self-generated tones. Additionally, this effect emerged for participants that perceived a large difference in their personal level of control between the high and low IoC condition, but not for participants experiencing a small difference. We thus showed that P2/3a amplitudes were not simply related to the presented ratio of desired to undesired sounds in the prior IoC training, but to the individual IoC this training induced. Likewise, the effects cannot be explained by differing motor identity associations between the desired sound and button presses induced by the presented ratios, as such a carryover effect should have been found for the N1 as well (Baess et al., 2008; Hughes et al., 2013). For the N1 though, no effect of the IoC was seen, which is also in line with the notion that early processing is more reflective of the classic mechanism of forward model predictions, which is not affected by prior belief information.

4.3 | Distinct late components for self-generated and external sounds?

From the grand-average ERPs obtained in the present study, it was quite obvious that the P2/P3a latency in the Act-sound condition was delayed relative to external sounds, and this difference between conditions was, indeed, significant (see supplementary materials). This is not a common finding in the literature, but an important difference in our compared to previous study designs is that only 50% of button presses were followed by sounds, while most self-generation paradigms entail a 100% probability. The P3a, as well as a later

P2 around 250 ms and thus in the latency range of the positive peak for self-generated sounds in the present study, have been associated with non-target stimuli in oddball tasks (Crowley & Colrain, 2004; Polich, 2007), suggesting that they reflect an orienting response to an unusual or novel stimulus. It is possible that the sounds following button presses in our paradigm prompted such an orientation response, as with a probability of 50% there was maximal uncertainty about whether a button press was followed by a sound or not. The later positive peak we observed for Act-sounds might, therefore, be explained not as a delay of the P2, but as an additional ERP component overlaying the reduced P2 we expected for the processing of Act-sounds. Interestingly, a similar pattern of an additional later component was seen in studies entailing also external sounds that were presented intermixed with the self-generated sound (Baess et al., 2011; Ghio et al., 2018). Specifically, visual inspection suggests that the late positive component for intermixed external sounds, which were presented in irregular intervals between self-generated sounds and less frequently (only in 40% of the trials), had a later peak compared to the more regular external sounds presented in a separate block. Accordingly, these findings could be interpreted in terms of an overlaying, additional ERP component reflecting an orientation response. The notion that the later positive peak for self-generated sounds in the present study reflects a separate ERP component is also supported by the different topography compared to the peak for externally generated sounds.

Considering that sounds in the IoC task were not just task relevant, but also accompanied by a monetary reward or penalty, they might have gained a strong intrinsic motivational significance for participants, which has been shown to enhance P3 amplitudes (Nieuwenhuis et al., 2011). In this respect, our results would imply that the desired sounds in the low P(O) block were associated with a greater personal significance, as P3 amplitudes in the high P(O) block were lower. This could be explained by the lower frequency of monetary rewards in the low P(O) block, which could have led to a high personal significance of the desired sounds as markers of reward, but this line of argument would require an additional control measure. However, the P2/P3 in our paradigm was not exclusively modulated by the frequency of the desired sound, as reflected by the factor P(O), but also by participants' subjective control ratings. It also has to be noted that if personal significance had been established as a property of the sound, Ext-sounds should exhibit a similar P3 as Act-sounds, as both conditions were presented after the IoC task.

While this pattern in the processing of self- and externally generated sounds should be further examined in future studies, it is important to note that the processing differences for self-generated sounds induced by different levels of IoC in the present study were found already between 160 and 200 ms after tone onset, in the time window centered on the P2/P3a peak for the processing of external sounds. It seems that IoC, and possibly agency, affects processing immediately after the typical N1 time window and thus after the efference-copy based comparison between predicted and actual sensory input.

4.4 | Limitations of the study

One concern in interpreting the results of the present study is that we cannot exclude that different expectation strengths for the upcoming tone stimuli caused the differential effect on the P2/3a in the high and low P(O) block. Even though the relationship of button presses and sounds in both IoC training conditions was non-contingent, desired sounds followed button presses much more often in the high IoC than in the low IoC condition. In the high IoC condition, a generally higher expectation of sounds occurring after button presses may thus have led to lower P2/P3a amplitudes, similar to studies in which P2 reductions for self-generated sounds were found when external sounds could be expected based on visual cues. This explanation for our findings seems unlikely, however, because the effect was not found for participants that perceived only small differences in their control over sound production between both conditions. It is of course still possible that interindividual differences in IoC only affected the expectation of sound appearance after button presses in the context of a higher-level prediction process, independently of judgments about the agency. It also must be noted that postdictive agency in our design was never ambiguous, as all sounds presented in the Act-sound condition were generated by the participants, and the cause-effect relationship was never questioned. In future examinations of predictive influences on the agency, perceived control should thus be manipulated in a self-generation paradigm without altering expectedness, while allowing uncertainty about the source of the produced stimuli.

4.5 | Conclusion

We induced either high or low IoC over the production of a sound in order to assess effects on the neural processing of this sound in a subsequent self-generation task, where it was either self-generated or not. We found no effect of the IoC on the N1 reduction for self- versus externally generated sounds, which is in line with the assumption that motor-related prediction mechanisms are reflected in this early processing stage. A reduction of the P2/3a was found when the perceived IoC was high. This suggests that the later processing stage is affected by predictive aspects underlying the judgments of the agency.

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AUTHOR CONTRIBUTION

Alexander Seidel: Data curation; Formal analysis; Investigation; Project administration; Software; Supervision; Validation; Visualization; Writing-original draft; Writing-review & editing. **Marta Ghio:** Conceptualization; Investigation; Methodology; Project administration; Supervision; Validation; Writing-original draft; Writing-review & editing. **Bettina Studer:** Conceptualization; Methodology; Writing-review & editing. **Christian Bellebaum:** Conceptualization; Supervision; Writing-review & editing.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.
Supplementary Material

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