

Exploring the role of motor and non-motor predictive mechanisms in sensory attenuation: Perceptual and neurophysiological findings

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ABSTRACT

Sounds that result from our own actions are perceptually and neurophysiologically attenuated compared to sounds with an external origin. This sensory attenuation phenomenon is commonly attributed to prediction processes implicated in motor control. However, accumulating evidence suggests that attenuation effects can also result from prediction processes beyond the motor domain. The aim of the present study was two-fold. First, we attempted to replicate the role of identity-specific motor predictions in sensory attenuation. Second, we set out to examine whether attenuation effects can be observed when tones cannot be predicted from preceding actions, but only from the non-motor cues accompanying them. Participants completed a two-alternative forced choice task on the loudness of tones whose pitch was congruent or incongruent with previously learned key-tone or cue-tone associations. No convincing evidence was observed for identity predictions on a perceptual level nor on a neurophysiological level. However, exploratory analyses revealed that attenuation was more pronounced for participants who first learned to rely on motor (instead of non-motor predictions). Together, these findings suggest that the role of motor identity predictions in sensory attenuation might have to be reconsidered.

1. Introduction

Self-produced sensations are perceived as less intense than externally produced sensations (Schafer and Marcus, 1973). This sensory attenuation effect is famously exemplified by our inability to tickle ourselves (Blakemore et al., 2000; Weiskrantz et al., 1971) and is imperative for successful interaction with the environment. Reduced processing of action-effects not only frees up resources to deal with novel information, but is also thought to aid in the distinction of self and other produced effects (Frith et al., 2000; Haggard and Tsakiris, 2009). Although sensory attenuation is commonly ascribed to predictive processes implicated in motor control (Blakemore et al., 1998, 1999, 2000; Frith et al., 2000), accumulating evidence suggests that it can also be observed in the absence of any actions, when events are predictable from a different source (Hughes et al., 2013a; Schröger et al., 2015). The present study examined how attenuation effects resulting from these more general (non-motor) predictive mechanisms compare to those resulting from action-based predictions.

While the differential processing of self-generated and externally generated effects is demonstrated across sensory modalities, the present study restricts itself to the auditory domain, which is most extensively studied (Hughes et al., 2013a). Sounds following one's own actions are systematically reduced in perceived loudness compared to sounds with

an external origin (Sato, 2009; Weiss et al., 2011a, 2011b; Weiss and Schütz-Bosbach, 2012). In addition, the N1 component of the auditory ERP, which is thought to reflect prediction error, has a smaller amplitude for self- versus externally induced sounds (Baess et al., 2008; Baess et al., 2011; Schafer and Marcus, 1973; Timm et al., 2013; Van Elk et al., 2014).

The aforementioned findings are generally alluded to as evidence for the role of motor prediction in sensory attenuation. Specifically, self-prepared movement is thought to be accompanied by a copy of the motor command (i.e., an efference copy) that can be used to predict action-effects and as such explain away, or attenuate, incoming sensory input. Seeing that only self-produced, but not externally-produced effects are accompanied by efference copies, only the former are attenuated (Frith et al., 2000). Importantly, however, the nature of typically employed designs (i.e., comparing self-produced versus other produced tones) obscures identification of the exact predictive mechanisms that underlie sensory attenuation. General interpretations of forward models presume that differences between the conditions result from *identity predictions*, that is, from predictions about the exact identity of an upcoming sound (Hughes et al., 2013a). However, other differences between the conditions, such as the predictability of the point in time in which the effect will occur (i.e., *temporal predictions*), might also account for the observations (see Hughes et al., 2013a for a

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review). Only a few studies have circumvented these issues and demonstrated the influence of isolated identity predictions by the direct comparison of self-produced tones that were either congruent or incongruent with previously learned associations (Hughes et al., 2013b; Kühn et al., 2011).

Sensory attenuation is not restricted to the motor domain and has also been observed as a function of non-motor predictions. For instance, N1 amplitudes are reduced for tones whose frequency can be predicted from a preceding pattern, compared to unpredicted (Lange, 2009) or mispredicted (Hsu et al., 2015) tones. Similar attenuation effects were reported for tones whose identity could be inferred from simple contingencies, such as when the identity of the second tone of a pair is identical to the first tone (Hsu et al., 2014a). However, there are also some studies that failed to observe non-motor identity prediction effects. In one study, for example, the N1 amplitude did not differ between cued tones whose identity was fixed (i.e., predictable) versus randomly chosen (Hsu et al., 2013). Another study even observed an enhanced (instead of a reduced) N1 amplitude for attended predictable (vs. unpredictable) tones, whereas no prediction effect was observed when participants were not attending to the tones (Hsu et al., 2014b). Notwithstanding their diverging nature, the aforementioned findings suggest that sensory attenuation effects are broader than can be accounted for solely by forward models implicated in motor control.

While attenuation effects resulting from motor and non-motor predictions have been shown in isolation, only a few studies (across sensory modalities) have attempted to compare them in terms of quality and magnitude. Some of these studies have observed comparable attenuation effects as a result of both prediction sources (Desantis et al., 2014), whereas other studies have failed to observe non-motor prediction effects (Cardoso-Leite et al., 2010; Richters and Eskew, 2009; Bednark et al., 2015).¹ The findings of these studies are difficult to interpret as they employ different designs and varying indices of attenuation. For instance, motor and non-motor prediction effects have been compared both across samples (Cardoso-Leite et al., 2010; Richters and Eskew, 2009) and within the same sample (Desantis et al., 2014; Bednark et al., 2015). Moreover, both neurophysiological (Bednark et al., 2015) and varying perceptual indices of attenuation have been employed, including measures of perceptual sensitivity (e.g., just noticeable difference, Desantis et al., 2014; and d' , Cardoso-Leite et al., 2010) as well as measures of perceptual intensity (e.g., point of subjective equality, Desantis et al., 2014). How these different indices of attenuation relate to each other is unclear, which complicates interpretations of the observed findings and the (dis)similarity between attenuation effects resulting from motor and non-motor prediction.

The aim of the present study was twofold. First, the current study served to determine the role of identity-specific motor predictions in attenuation. Second, we wished to examine whether non-motor predictions can take over and result in similar attenuation effects when motor predictions have no predictive value. To circumvent the aforementioned issues regarding design related differences across studies, we directly compared motor and non-motor prediction effects in the same sample of subjects, using frequently employed measures of neurophysiological attenuation (i.e., N1 amplitude) as well as perceptual intensity and perceptual sensitivity indices.

To examine the influence of predictive processes on attenuation, participants completed an adaptation of an existing auditory detection paradigm (Desantis et al., 2014) consisting of a motor prediction and a non-motor prediction block. The order of these blocks was counter-balanced across participants. In the first phase of the task, participants were exposed to contingencies between freely chosen key-presses (motor prediction block) or geometrical stimuli accompanying these key presses (non-motor prediction block) and the pitch of a subsequent

tone. In the subsequent test phase, we examined perceived loudness as a function of action-congruency (i.e., comparing tones that were congruent versus incongruent with previously learned relationships). Based on the studies outlined above, we at least expected lower perceived intensity, sensitivity and a decreased N1 amplitude for tones that were congruent (vs. incongruent) with previously learned action-effect associations. Whether or not a similar pattern would be observed for the non-motor prediction condition was more difficult to predict given the ambiguity of the existing literature regarding the effects of non-motor prediction cues on sensory attenuation.

2. Experimental procedure

2.1. Participants

Twenty-four participants took part in the experiment ($M_{age} = 20.63$; $SD_{age} = 2.45$; 15 females; 19 right-handed).² All participants had self-reported normal or corrected to normal vision and no hearing disabilities. In addition, none of the participants were smokers or recreational drug users and none reported current neurological conditions, mental illnesses or use of psychiatric medication. Participants were requested to refrain from caffeine consumption three hours prior to the experiment. All participants received written and oral information concerning the set-up of the experiment and signed an informed consent form. A monetary reimbursement was received in return for participation. The study received approval from the faculty's (Social and Behavioral Sciences) ethical board.

2.2. Procedure

Participants completed a modified version of an auditory detection paradigm as described in Desantis et al. (2014). The task consisted of a motor prediction block and a non-motor prediction block with a five-minute break in-between. The order of these blocks was counter-balanced between participants. Within each block participants completed ten acquisition phases (A), each consisting of 80 trials, and ten test phases (T), each consisting of 36 trials. These phases were presented in an interleaved (ATAT) order to reduce the likelihood of extinction effects. The acquisition phase served to learn associations between actions and tones (motor prediction block) or between visual cues and tones (non-motor prediction block). In the test phase, the effect of the learned associations on loudness perception was assessed. In order to diminish attention lapses, participants played Tetris (Petrus; Pfister, 2008³) for three minutes after completing half of the motor block and after half of the non-motor prediction block. Prior to the start of the motor and non-motor prediction block participants completed practice trials for both the acquisition phase (8 trials) and the test phase (4 trials). After the experiment, participants answered some general exit questions, including questions about handedness and demographic characteristics.

2.3. Task

2.3.1. Acquisition phase

Participants were instructed to produce a freely chosen right or left key press in response to a white fixation cross. Key presses were produced by pressing the left or right button on a Cedrus RB530 response pad (Cedrus Corporation, San Pedro, CA) with the corresponding index finger.⁴ Participants were asked to aim for an equal response

¹ Bednark et al. (2015) did not observe any N1 attenuation related to identity-specific predictions, irrespective of prediction source.

² Three participants were excluded prior to data analysis due to a technical error and one participant for not adhering to task instructions. Four new participants were recruited and assigned to the respective cells of the design. Demographics regard the final sample.

³ Traditional Tetris sounds were added to this version of Tetris.

distribution. Every twenty trials feedback regarding the ratio of key presses was presented to assist participants in this attempt. In the motor prediction condition, each key press (motor cue) generated a tone after a 200-ms interval. For half of the participants, a left key press was associated with a low tone and a right key press was associated with a high tone. The opposite key-tone mapping applied to the other half of the participants. Participants were made explicitly aware of these associations prior to the start of each phase. In the non-motor prediction condition, key presses were immediately followed by either a white square or a white circle (non-motor cue) that was presented for 100 ms. After a 100-millisecond interval a low or a high tone was presented. Importantly, the geometrical stimulus, and not the key press, predicted the tone pitch in this condition. There was no association between geometrical stimuli and key presses on a phase level. Similar to the motor prediction condition, cue-tone mappings were counterbalanced between participants. All tones were 100 millisecond lasting sine waves, including 10 millisecond onset and offset envelopes. The tones were presented binaurally at approximately 74 dB through foam in-earplugs (Earlink 3A Oty 50, Aeero Company Auditory Systems, Indianapolis, IN, USA). Two pairs comprising a low and a high tone frequency were counterbalanced between blocks and participants to reduce the likelihood of spill-over of learning effects from the motor to the non-motor prediction block (or vice versa). Accordingly, for half of the participants a low tone of 750 Hz and a high tone of 900 Hz were presented in the motor prediction block and a low tone of 700 Hz and a high tone of 850 Hz were presented in the non-motor prediction block. The opposite ascription applied to the other half of the participants. All trials were separated by a 1000 ms inter-trial interval.

Each acquisition phase consisted of 80 trials (similar to Desantis et al., 2014), including 20% of catch trials. The catch trials were identical to the main acquisition trials, with the exception that participants had to indicate the frequency of the presented tone (low or high) by pressing one of two foot pedals. In the motor prediction condition the labels of the foot pedals always matched learned associations. That is, if participants learned that a left key press was associated with a low tone, the label of the left pedal also corresponded to a low tone. In the non-motor prediction condition foot pedals labels were counterbalanced in a similar manner, such that for half of the participants the left pedal represented a low tone and the right pedal a high tone, whereas the opposite labeling applied to the other half of the participants.

2.3.2. Test phase

In the test phase participants were again instructed to generate freely chosen key presses as soon as a white fixation cross was presented. Similar to the acquisition phase the key press (motor) or the visual cue (non-motor) was followed by an approximately 74 dB tone. Importantly, however, the tones were now presented randomly such that the frequency of the tones was either congruent, or incongruent with learned action-effect or cue-effect associations. In addition, this (standard) tone was now followed by a second (sample) tone of equal frequency but varying loudness (~70–78 dB, with 1 dB intervals) after an interval of 1100 ms. Participants completed a two-alternative forced choice task, in which they indicated whether the first or second tone was louder by using the foot pedals. The left foot pedal always indicated that the first tone was loudest, whereas the right foot pedal always indicated that the second tone was loudest. The ascription of frequency pairs to the motor and non-motor prediction block was identical to the acquisition phase. Fig. 1 depicts the timeline of acquisition and test

trials.

To ensure an approximately equal distribution of congruent and incongruent trials across congruency and sample tone levels, a list was pre-programmed for each key press (in the motor prediction condition) and for each cue (in the non-motor prediction condition). This list contained two congruent and two incongruent trials for each level of the sample tone. Trials were randomly sampled from this list without replacement until all the aforementioned combinations were shown, and were reset as soon as list length was exceeded. This approach prevents unequal pairing between one of the predictive cues and congruency levels (e.g., more pairings of the left key with congruent trials compared to the right key), and also results in the same number of trials for each sample tone magnitude per congruency level – provided that participants press each key equally often. To ensure an equal response distribution, participants received feedback regarding the proportion of left and right key presses during the task.⁵ All participants were able to achieve an approximately equal distribution across test phases (Motor prediction condition, right key presses: $M = 50.24\%$, $SD = 1.86\%$; Non-motor prediction condition, right key presses: $M = 49.80\%$, $SD = 1.97\%$).

2.4. EEG recording

EEG was recorded with the Biosemi Active Two EEG system (BioSemi, Amsterdam) from 64 electrodes (sampling rate: 2048 Hz) that were positioned according to the international 10/20 system. An online Common Mode Sense-Driven Right Leg (CMS-DRL) was used as a reference. Electro-oculogram (EOG) was measured from electrodes placed on the suborbit and supraorbit of the right eye and on the outer canthi of both eyes.

2.5. Data pre-processing

2.5.1. Behavioral data: test trials

Trials with erroneous responses (i.e., multiple key presses, multiple pedal presses, pressing a pedal when a key was supposed to be pressed or vice versa) were excluded from all analyses ($M = 4.81\%$, $SD = 2.95\%$). In addition, data inspection indicated that participants were occasionally very slow to respond to the fixation cross at the start of the trial, as well as to judge which of the two tones was louder. These delayed responses are problematic as, in the first case, participants might not have attended properly to the stimuli, whereas, in the latter case, information as to which tone was louder might no longer be accessible. For these reasons, we decided to reject trials when the onset time of key presses ($M = 1.85\%$, $SD = 0.51\%$) and/or pedal responses ($M = 2.00\%$, $SD = 0.54\%$) were more than 3 standard deviations above the mean of that participant (after first excluding trials with multiple responses). The mean number of trials per condition that was contained for the final analysis is presented in Table 1.

2.5.2. Behavioral data: catch trials

Similar to the test trials, trials with multiple responses ($M = 4.39\%$, $SD = 2.60\%$) or extreme reaction times for hand ($M = 1.64\%$, $SD = 0.48\%$) and/or pedal responses ($M = 1.88\%$, $SD = 0.57\%$) were excluded prior to further analysis. The average percentage of the remaining trials was 92.37% ($SD = 3.79\%$) for the motor prediction condition, and 92.32% ($SD = 3.10\%$) for the non-motor prediction condition.

⁴ One participant indicated to have used thumbs instead of index fingers to press the keys during both the acquisition and the test phase of the motor prediction block (first block for this participant). We decided against excluding this participant considering that the mapping of importance was hand-specific (e.g., left – low; right – high) and not necessarily finger-specific.

⁵ Due to a small programming error the feedback regarding the key press distribution was occasionally incorrect in the test phase (but not in the acquisition phase). Importantly, this error did not seem to have a considerable impact on participants considering that they pressed both keys approximately equally often.

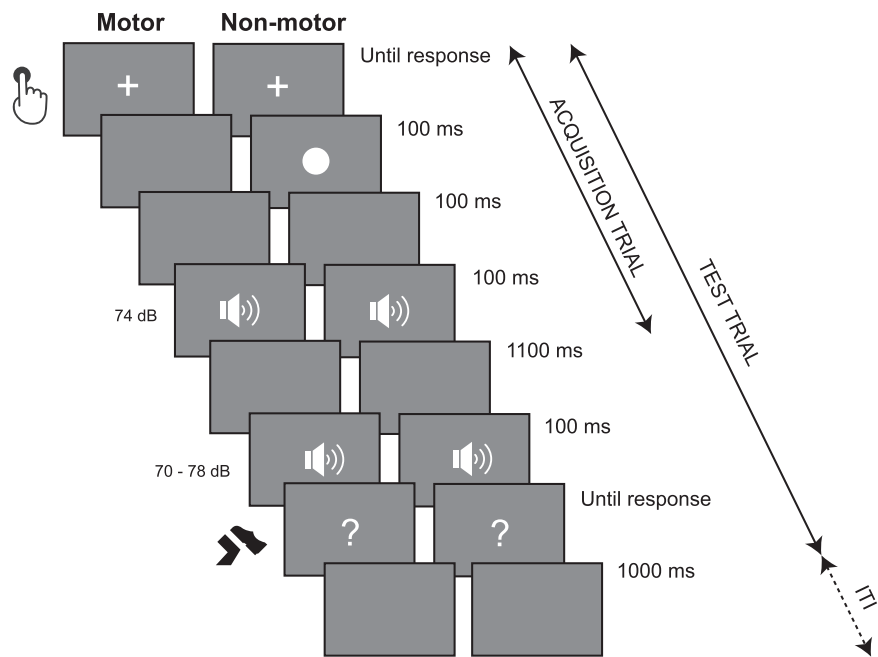


Fig. 1. Timeline of acquisition and test trials as a function of prediction type.

Table 1
Mean number of trials used for final analysis as a function of prediction type, congruency and sample tone magnitude.

Prediction type	Congruency	Sample tone (dB)								
		70	71	72	73	74	75	76	77	78
Motor	Congruent	18.38 (1.66)	17.79 (1.22)	18.75 (1.78)	18.33 (1.83)	17.75 (1.70)	17.88 (1.26)	18.58 (1.41)	18.75 (1.42)	18.00 (1.89)
	Incongruent	17.58 (1.89)	18.42 (1.28)	18.33 (1.63)	17.83 (1.99)	18.13 (1.70)	18.21 (1.82)	18.50 (2.09)	18.92 (1.67)	18.38 (1.21)
Non-Motor	Congruent	18.25 (1.26)	18.33 (1.76)	18.33 (1.40)	17.71 (1.90)	17.58 (1.38)	18.75 (1.48)	18.75 (1.54)	18.67 (1.69)	18.79 (1.25)
	Incongruent	18.92 (1.14)	18.38 (1.44)	18.08 (1.89)	17.88 (1.75)	17.83 (1.13)	18.25 (1.51)	18.58 (1.21)	18.96 (1.12)	18.92 (1.18)

Note. Numbers between parentheses represent standard deviations.

2.5.3. EEG data

Offline, the data was downsampled to 256 Hz, bandpass filtered (1–25 Hz), re-referenced to the average reference and segmented into epochs from – 200 to 500 ms relative to the onset of the first tone. Ocular artifacts were rejected using the EOG signal (Gratton et al., 1983). Trials with extreme and incorrect responses were excluded based on the criteria described in Section 2.5.1. Remaining artifacts were excluded by automatically rejecting segments with signals exceeding +/– 75 microvolts on channels of interest (see Section 2.6.2). Baseline correction was applied using an interval of 100 ms prior to the first tone. An average percentage of approximately ninety percent of the trials was contained for final analyses in all the conditions (Motor prediction, congruent: $M = 89.55\%$, $SD = 4.61\%$; Motor prediction, incongruent: $M = 89.40\%$, $SD = 4.31\%$; Non-motor prediction, congruent: $M = 89.40\%$, $SD = 4.58\%$; Non-motor prediction, incongruent: $M = 90.25\%$, $SD = 3.61\%$).⁶

⁶ For one participant 21 trials were missing in the motor condition due to a technical malfunction. The reported percentages were calculated based on the remaining trials.

2.6. Data analysis

2.6.1. Perceptual attenuation

The percentage of “second-tone-is-louder” responses was calculated separately for each combination of prediction type, congruency and magnitude of the second (sample) tone for each individual participant. These percentages were fitted with a psychometric function (cumulative Gaussian) to calculate indices of perceptual intensity (point of subjective equality) and perceptual sensitivity (just noticeable difference); see Fig. 2. The point of subjective equality (PSE) represents the sample tone magnitude at which the sample tone is perceived as louder than the standard tone on fifty percent of the trials. Accordingly, a lower PSE value corresponds to more attenuation of the standard tone (i.e., the first tone following the predictive cue). In addition to the PSE, previous studies on attenuation have often included the just noticeable difference (JND), which is half of the difference of the sample tone magnitude at which the sample tone is judged as louder than the standard tone on 75% of the trials and on 25% of the trials. This index is thought to represent perceptual sensitivity and reflects the variability of responses given by the participant.

2.6.2. Neurophysiological attenuation

Given that the N1 is known to consist of several separate peaks, the ERP analysis focused on three peaks (N1a, N1b and N1c; Näätänen and

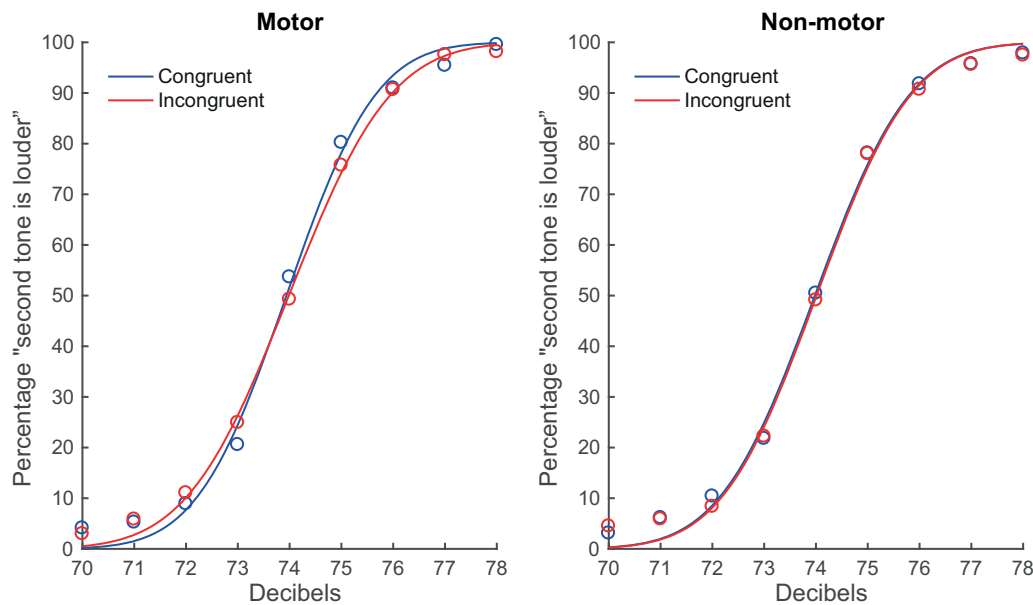


Fig. 2. Average percentage of “second-tone-is-louder” responses for congruent and incongruent trials, as a function of sample tone magnitude and prediction type across all participants. The presented percentages were calculated excluding erroneous trials and outliers (see Section 2.5.1).

Picton, 1987; Woods, 1995) that have previously examined in the context of motor prediction (c.f. Timm et al., 2013; Sanmiguel et al., 2013). The N1b peak maximizes over frontocentral electrodes, whereas the N1a and N1c peaks are maximal over bilateral mid-temporal electrodes (Woods, 1995). Given these differences in topography and latency, congruency and prediction type effects were assessed separately for each peak. Specifically, amplitudes were averaged across frontocentral electrodes (Cz, FCz and Fz) for the N1b peak, and across left (C5, FC5, FT7 and T7) and right (C6, FC6, FT8 and T8) mid-temporal electrodes for the N1a and N1c peaks. The time windows of interest were determined based on the observed grand averages. The N1a and N1c peak were defined as the first (60–100 ms) and second (120–170 ms) negative peak on the temporal electrodes, respectively. The N1b was analyzed in a window stretching from 80 to 130 after tone onset. All peaks were quantified as the most negative amplitude for individual averages within the previously specified windows. Separate repeated measures ANOVA's were conducted for each component with prediction type (motor versus non-motor) and congruency (congruent versus incongruent), as independent variables.

3. Results

3.1. Catch trial accuracy

Catch trial accuracy was high for all four tones: 700 Hz: $M_{acc} = 0.98$, $SD_{acc} = 0.04$; 750 Hz: $M_{acc} = 0.97$, $SD_{acc} = 0.03$; 850 Hz: $M_{acc} = 0.97$, $SD_{acc} = 0.06$; 900 Hz: $M_{acc} = 0.97$, $SD_{acc} = 0.03$. These results indicate that participants paid attention to the tones and were well able to identify them.

3.2. Perceptual attenuation

3.2.1. Point of subjective equality

To examine the hypothesized effects of prediction on perceptual intensity, PSE values were subjected to a repeated measures ANOVA with prediction type (motor versus non-motor) and congruency (congruent versus incongruent) as independent variables. This analyses yielded no main effects of prediction type, $F(1,23) = 0.13$, $p = .721$, $\eta_p^2 = 0.01$ and congruency, $F(1,23) = 0.16$, $p = .692$, $\eta_p^2 = 0.01$, nor an interaction between these two factors $F(1,23) = 0.03$, $p = .866$,

$\eta_p^2 < 0.01$.

In order to examine to what extent these non-significant findings reflect evidence for the null hypothesis we calculated Bayes factors for the reported effects, using the R package Bain (Gu et al., 2018; <https://informative-hypotheses.sites.uu.nl/software/bain/>). This package differs from other, more generally known, software (e.g., JASP), in that it specifies the prior width based on a fraction of the data. In addition, instead of running omnibus tests, Bain allows one to specify the exact contrast of interest. Note that for the current study this results in separate evaluations of evidence for the main and interaction effects. The analyses for the main effects revealed that the observed data is about four times as likely under the null hypothesis compared to the alternative hypothesis⁷ for both prediction type ($BF_{01} = 4.59$) and congruency ($BF_{01} = 4.52$). In addition, the evidence for the absence of an interaction effect is almost five times as likely as the evidence for the presence of an interaction effect ($BF_{01} = 4.83$).

An additional, exploratory analysis was conducted to examine whether differences in preceding predictive context (e.g., the order in which the prediction type blocks were shown) might have affected the results. A three way mixed ANOVA was executed, with order of the prediction type blocks (motor first versus non-motor first) as an additional between-subject variable. This analysis yielded a significant interaction between congruency and order, $F(1,22) = 5.66$, $p = .027$, $\eta_p^2 = 0.20$. As depicted in Fig. 3, PSE values were descriptively lower for the congruent compared to the incongruent condition if participants started with the motor prediction block, $F(1,22) = 3.97$, $p = .059$, $\eta_p^2 = 0.15$, whereas an opposite, albeit weaker, pattern was observed for participants who started with the non-motor prediction block, $F(1,22) = 1.88$, $p = .184$, $\eta_p^2 = 0.08$.⁸ Notably, there was no three-way interaction between prediction type, order and congruency, F

⁷ For all the reported Bayesian analyses the null hypothesis refers to the absence of a main or interaction effect, whereas the alternative hypothesis refers to the presence of a main or interaction effect.

⁸ Considering the sensitivity of small samples for outliers, we further evaluated the simple main effects of congruency using separate Wilcoxon signed-rank tests for each level of order. The same pattern of results was observed. That is, the effect of congruency was marginally significant for participants who started with the motor prediction block ($V = 20$, $p = .08$, one-tailed), whilst the effect for participants who started with the non-motor prediction block was not significant ($V = 58$, $p = .94$, one-tailed).

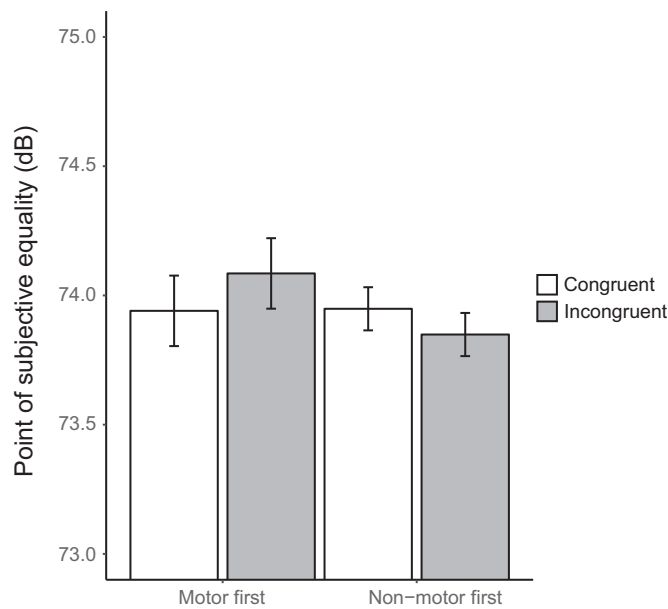


Fig. 3. Point of subjective equality as a function of congruency and block order (collapsed over prediction type). Error bars reflect within-subject 95% confidence intervals calculated according to Morey's (2008) method.

(1,22) = 0.31, $p = .583$, $\eta_p^2 = 0.01$, indicating that the observed order effect was similar in the motor and in the non-motor prediction condition.

3.2.2. Just noticeable difference

A separate 2 (prediction type: motor versus non-motor) \times 2 (congruency: congruent versus incongruent) repeated measures ANOVA was conducted on the JND values. This analysis yielded no main effects of prediction type, $F(1,23) = 0.20$, $p = .663$, $\eta_p^2 = 0.01$ and congruency, $F(1,23) = 2.76$, $p = .110$, $\eta_p^2 = 0.11$, nor an interaction between prediction type and congruency $F(1,23) = 0.30$, $p = .591$, $\eta_p^2 = 0.01$.

We further examined these non-significant effects by calculating Bayes factors. Bayesian analyses revealed that the observed data is about four times more likely in the absence of a main effect of prediction type, than in the presence of such an effect ($BF_{01} = 4.44$). The same is true for the interaction effect between prediction type and congruency ($BF_{01} = 4.22$). However, the evidence for an effect of congruency is inconclusive (i.e., neither evidence for the null or for the alternative hypothesis is obtained; $BF_{01} = 1.24$).

Contrary to the PSE analysis, the exploratory addition of order to the design did not yield an interaction between congruency and order, $F(1,22) < 0.01$, $p = .973$, $\eta_p^2 < 0.01$. The three-way interaction between prediction type, congruency and order, also did not reach significance, $F(1,22) = 0.03$, $p = .866$, $\eta_p^2 < 0.01$.

3.3. Neurophysiological attenuation

Grand average ERP's and voltage maps for the N1a, N1b and N1c components are shown separately for the motor- and non-motor prediction condition in Fig. 4.

3.3.1. N1b

The analysis for the N1b time window revealed no significant main effect for congruency, $F(1,23) = 1.19$, $p = .287$, $\eta_p^2 = 0.05$, no significant main effect for prediction type, $F(1,23) = 0.29$, $p = .595$, $\eta_p^2 = 0.01$, and no significant interaction between congruency and prediction type, $F(1,23) = 0.02$, $p = .889$, $\eta_p^2 < 0.01$.

Similar to the analysis of the behavioral data, we conducted

Bayesian analyses to evaluate to what extent the non-significant findings reflect evidence for the null hypothesis. The observed data is about four times as likely under the null hypothesis compared to the alternative hypothesis for both the main effect of prediction type, as well as for the interaction between prediction type and congruency (see Table 2). In addition, the data is almost three times as likely under the hypothesis that there is no difference between congruent and incongruent conditions, than under the hypothesis that there is a difference between these conditions. Potential effects of predictive context were explored by adding order (motor-prediction condition first versus non-motor prediction condition first) to the design as a between subject factor. However, no significant interactions with this factor were observed (see Table 3).

3.3.2. N1a

Similar to the N1b time window, no significant main effect for prediction type, $F(1,23) = 0.12$, $p = .735$, $\eta_p^2 = 0.01$, or congruency, $F(1,23) = 2.66$, $p = .116$, $\eta_p^2 = 0.10$, nor a significant interaction between prediction type and congruency, $F(1,23) = 0.82$, $p = .374$, $\eta_p^2 = 0.03$, was observed for the N1a window. The main effect of laterality was significant, $F(1,23) = 4.46$, $p = .046$, $\eta_p^2 = 0.16$, showing a higher N1a amplitude for left electrodes ($M = -0.73$, $SE = 0.14$) compared to right electrodes ($M = -0.38$, $SE = 0.14$). Given that this main effect was not qualified by interactions with congruency, $F(1,23) = 3.05$, $p = .094$, $\eta_p^2 = 0.12$, prediction type, $F(1,23) = 0.26$, $p = .615$, $\eta_p^2 = 0.01$, or congruency and prediction type, $F(1,23) = 0.10$, $p = .751$, $\eta_p^2 < 0.01$, we decided to collapse the data across laterality levels prior to calculating Bayes factors (see Table 2) and exploring effects of order (see Table 3).

Bayesian analyses revealed that the data is about four times more likely under the hypothesis that there is no difference between the motor and the non-motor prediction condition, than that under the hypothesis there is a difference between these conditions. In contrast, the evidence for the main effect of congruency is inconclusive. Finally, the data points towards the absence of an interaction effect (see Table 2).

The exploratory analyses including order yielded a significant three way interaction between prediction type, congruency and order, $F(1,22) = 4.46$, $p = .046$, $\eta_p^2 = 0.17$. In order to further explore this interaction, we examined the simple interaction effect between prediction type and congruency at each level of order. As can be seen in Fig. 5, the interaction between prediction type and congruency was more pronounced for participants who started the experiment with the motor prediction condition, $F(1,22) = 4.75$, $p = .040$, $\eta_p^2 = 0.18$, than for participants who started with the non-motor prediction condition, $F(1,22) = 0.65$, $p = .429$, $\eta_p^2 = 0.03$. For participants who started with the motor condition, an expected reduction in N1 amplitude for congruent versus incongruent trials was observed for the non-motor prediction condition, $F(1,22) = 7.42$, $p = .012$, $\eta_p^2 = 0.25$, but not for the motor prediction condition, $F(1,22) < 0.01$, $p = .965$, $\eta_p^2 < 0.01$.⁹ Note that these results roughly mimic the observed pattern of the PSE values, in the sense that congruency effects were restricted to participants who started with the motor prediction condition. However, unlike perceptual attenuation effects, the order effects seem to be driven by the non-motor prediction condition on a neurophysiological level.

⁹ Non-parametric Wilcoxon signed-ranked tests provided evidence for a similar pattern of second order simple main effects. Specifically, for participants who started with the motor condition, a significant effect of congruency was observed in the non-motor prediction condition ($V = 65$, $p = .02$, one-tailed), whereas there was no significant difference between congruent and incongruent trials in the motor prediction condition ($V = 40$, $p = .48$, one-tailed).

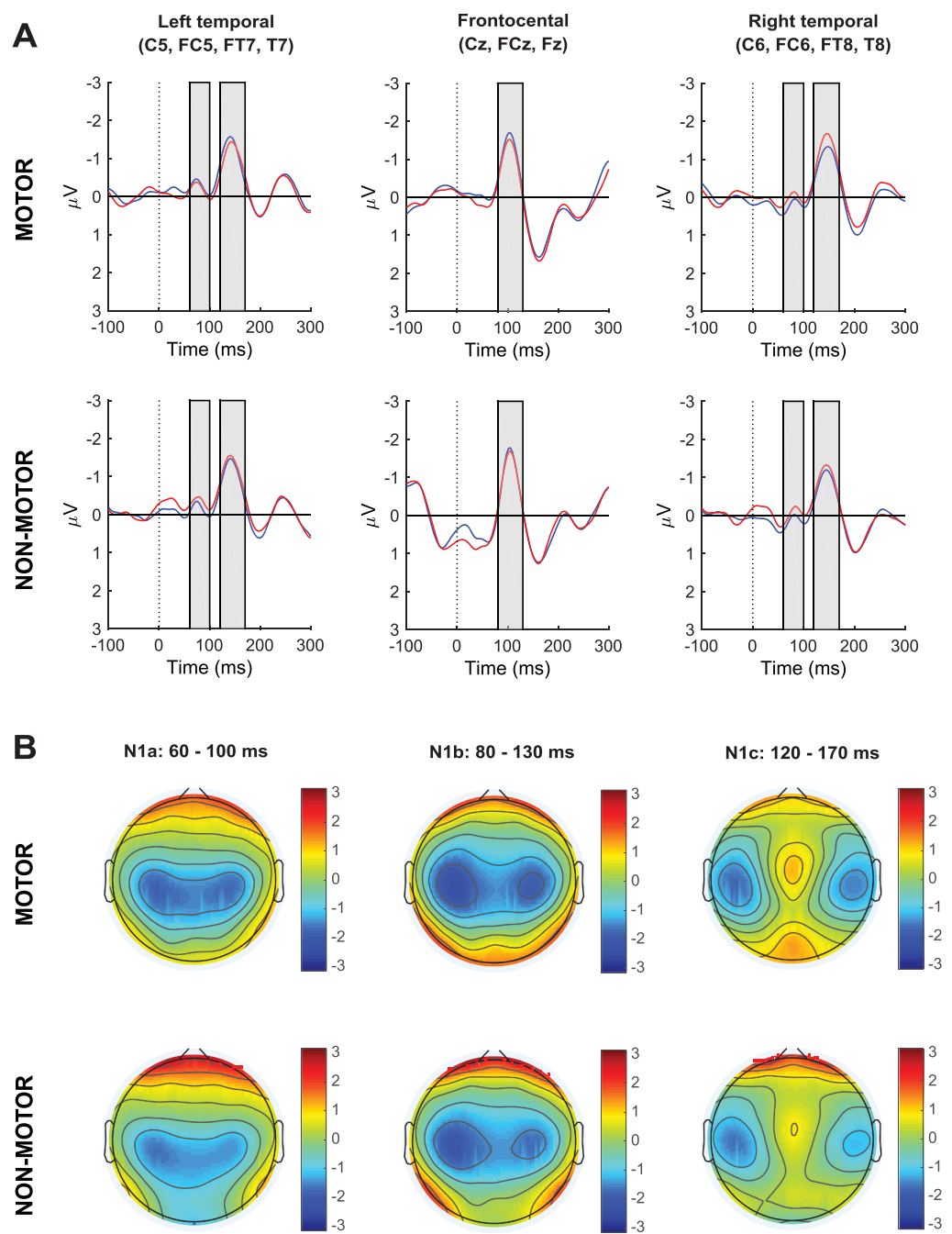


Fig. 4. (A) Grand average ERP's over congruent (blue lines) and incongruent (red lines) trials in the motor- and the non-motor prediction condition. Grey areas represent time windows subjected to statistical analysis. (B) Topographic maps of the motor- and non-motor prediction conditions (collapsed over congruency). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

Table 2			
Evidence for the absence of effects (reflected by BF ₀₁) for all N1 peaks.			
	N1a (60–100 ms)	N1b (80–130 ms)	N1c (120–170 ms)
Prediction type	4.62	4.24	4.23
Congruency	1.29	2.71	2.36
Prediction type × Congruency	3.25	4.85	3.80

3.3.3. N1c

We observed no significant main effects for congruency, $F(1,23) = 1.46, p = .239, \eta_p^2 = 0.06$ and prediction type, $F(1,23) = 0.30, p = .592, \eta_p^2 = 0.01$, nor a significant interaction between congruency and prediction type, $F(1,23) = 0.51, p = .483, \eta_p^2 = 0.02$. In addition, we observed no main effect for laterality, $F(1,23) = 0.59, p = .449, \eta_p^2 = 0.03$, no interaction effect between prediction type and laterality, $F(1,23) = 1.43, p = .245, \eta_p^2 = 0.06$, and no interaction effect between

Table 3
Results of mixed-ANOVA's including order for all N1 peaks.

	N1a (60–100 ms)			N1b (80–130 ms)			N1c (120–170 ms)		
	<i>F</i>	<i>p</i>	η_p^2	<i>F</i>	<i>p</i>	η_p^2	<i>F</i>	<i>p</i>	η_p^2
Prediction type	0.11	.740	< 0.01	0.29	.593	0.01	0.29	.595	0.01
Congruency	2.76	.111	0.11	1.28	.270	0.06	1.50	.234	0.06
Prediction type \times Congruency	0.95	.342	0.04	0.02	.888	< 0.01	0.55	.468	0.02
Order	1.81	.192	0.08	1.27	.271	0.06	0.07	.802	< 0.01
Order \times Prediction type	0.10	.750	0.01	1.36	.256	0.06	0.64	.433	0.03
Order \times Congruency	1.83	.190	0.08	2.78	.109	0.11	1.59	.220	0.07
Order \times Congruency \times Prediction type	4.46	.046*	0.17	1.21	.283	0.05	2.60	.121	0.11

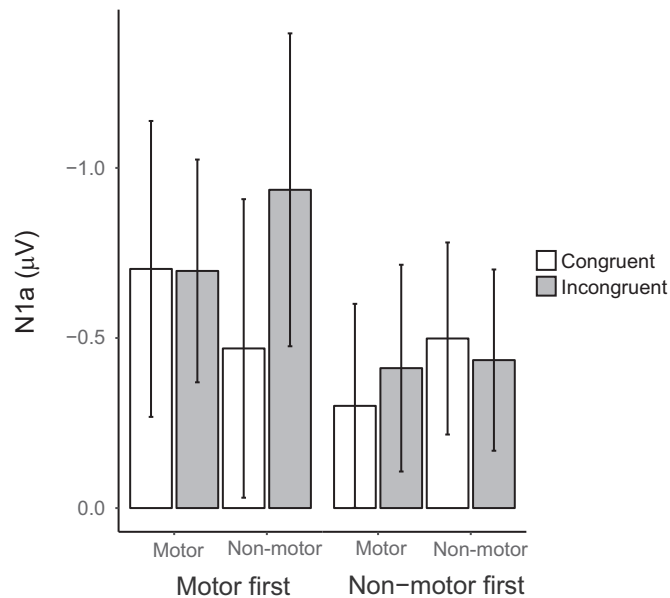


Fig. 5. N1a amplitude as a function of prediction type, congruency and block order. Error bars reflect within-subject 95% confidence intervals calculated according to [Morey's \(2008\)](#) method.

congruency and laterality, $F(1,23) = 3.22$, $p = .086$, $\eta_p^2 = 0.12$. The interaction between prediction type, congruency and laterality also did not reach significance, $F(1,23) = 4.02$, $p = .057$, $\eta_p^2 = 0.15$. Given the absence of laterality effects, the data was collapsed prior to Bayesian analyses and exploratory analyses including order.

Bayesian analyses yielded substantial evidence for the absence of a main effect of prediction type and for an interaction effect between prediction type and congruency. Although the evidence for the absence of a main effect of congruency is not substantial, it is still stronger than evidence for the presence of such an effect. None of the interaction effects including order reach significance (see [Table 3](#)).

4. Discussion

In an attempt to reconcile divergent findings in the literature regarding the similarity of attenuation effects resulting from motor and non-motor prediction, the present study directly compared these prediction effects in the same sample of subjects while employing frequently used indices of perceptual and neurophysiological attenuation. Overall, none of the indices of attenuation displayed the expected difference between tones that were prediction congruent (versus incongruent). Surprisingly, however, exploratory analyses revealed that the expected congruency effect could be observed on some of the measures (PSE and N1a component) for a subset of participants who started the experiment by learning action-effect (instead of cue-effect)

relationships. Although these findings provide some support for the role of both motor- and non-motor identity prediction in attenuation, prediction-related effects were relatively weak and seemed to be conditional upon the person's learning history. Below we discuss our results in the context of the existing literature.

4.1. Perceptual attenuation

In contrast to our expectations, perceptual attenuation effects were only reflected in the point of subjective equality and were restricted to participants who completed the task in a specific block-order (i.e., starting with the motor prediction block). No statistical differences between prediction congruent and incongruent tones were observed for the just noticeable difference (JND). Importantly, however, Bayesian analyses revealed that the present data neither yields evidence for the alternative hypothesis, nor for the null hypothesis. According, the data do not allow for any further conclusions regarding the congruency effect on just noticeable difference values.

The finding that perceptual attenuation could only be observed for participants who completed the task in a specific block-order was not part of our initial expectations. Nevertheless, we wish to speculate about two subtle differences between the motor and non-motor prediction condition that might have contributed to this effect. Firstly, the mere presence of motor predictive cues was task relevant in the motor prediction block, as participants consistently had to choose which action to perform to produce a tone. In contrast, the non-motor predictive cues had no clear task relevance in the non-motor prediction block, where the identity of upcoming tones was determined by incidentally presented visual cues that occurred alongside non-predictive actions. As a consequence, attention towards actions and accompanying cues, as well as their relationship with subsequent effects, might have been reduced in non-motor prediction blocks compared to motor prediction blocks (see also, [Hughes et al., 2013a](#)). Since biases in information processing can be transferred from one task to another ([Wylie and Allport, 2000](#)), this difference in attentional tuning might not only have affected the acquisition of predictive relationships within each block, but might also have spilled over to the subsequent prediction block, explaining block order-dependent differences in attenuation.

Although speculative, this post-hoc explanation concurs with research on learned irrelevance, in which the associability of a cue has been shown to be impaired when it lacked predictive value in a preceding task ([Kruschke and Blair, 2000](#); [Le Pelley and McLaren, 2003](#)). This phenomenon is commonly attributed to the idea that participants learn that a cue is irrelevant and consequently spend less attention to it, which in turn interferes with the formation of associations with new outcomes ([Mackintosh, 1975](#)). In a similar vein, it has been demonstrated that attention to predictive relationships in one task can affect learning of such relationships in another task ([Custers and Aarts, 2011](#)). In particular, participants were more likely to learn unidirectional than bidirectional relationships when their attention was tuned to predictive (unidirectional) relationships in a prior unrelated task. Similarly, participants who started with the motor prediction block in the present

study might have paid attention to predictive relationships, allowing them to pick up on the cue-tone associations in the non-motor prediction block. In contrast, participants who started with the non-motor prediction block presumably lacked this attentional tuning, which interfered with further predictive learning in the motor prediction block.

In addition to differences in attentional tuning, a second explanation for the observed block-order effect pertains to an asymmetry in the number of potential predictive sources that was included in the motor and non-motor prediction block. Whereas the motor prediction block only contained actions, the non-motor prediction block included both actions as well as visual cues. As a result of this asymmetry, the transition from the first to the second block differed in terms of prediction errors, depending on what was learned first. Specifically, for participants who started with the motor prediction block, the transition to the non-motor prediction block likely resulted in pitch misprediction, as actions that previously fully predicted the frequency of one specific (low or high) tone were now followed by both (low and high) tone frequencies. In contrast, when transitioning from a non-motor prediction block to a motor prediction block, previously predictive non-motor cues were absent, rendering prediction errors unlikely. Given the known role of prediction errors in new learning (e.g., Pearce and Hall, 1980), it is likely that participants who started with the motor prediction block were more attuned to seeking new predictors of the tones in the second block (in this case the non-motor cues) as opposed to participants who started with the non-motor prediction block. This active learning advantage might in turn have resulted in stronger predictions and attenuation effects for the former participants.

Altogether, the learning history of participants, and resulting effects on attention allocation, might thus be moderating conditions for the contribution of identity prediction to attenuation. The potential importance of attention to predictive relationships is supported by recent research suggesting that attenuation results from a shift of attention to surprising (incongruent) events, instead of cancellation of expected congruent events (Yon and Press, 2017). Future work incorporating indices of learning and attention would be valuable to further examine to what extent these factors might explain the mixed results regarding prediction effects in the literature.

Notably, the observed order effect was present in both the motor and the non-motor prediction condition. In other words, no difference between action-based and cue-based expectations was observed. This concurs with previous research that has observed comparable effects for both prediction sources (Desantis et al., 2014), and suggests that attenuation effects might reflect a more general predictive mechanism rather than self-specific motor predictions. In line with this idea, a recent study demonstrated that the common neurophysiological attenuation of self- versus externally produced tones disappeared when the onset of the tone was made predictable by a preceding visual countdown (Kaiser and Schütz-Bosbach, 2018, although see: Weiss and Schütz-Bosbach, 2012). Combined with the current findings, these observations call into question the frequently proposed contribution of sensory attenuation to the sense of agency in general and self-other distinction in particular (e.g. Haggard and Tsakiris, 2009).

4.2. Neurophysiological attenuation

The perceptual results were roughly mimicked on a neurophysiological level. Firstly, no general statistically significant congruency effects were observed on any of the three N1 components. However, although the Bayesian analyses generally indicated that the data provided evidence for the null hypothesis, this evidence was not substantial for the N1b and N1c peak, and inconclusive for the N1a peak. These findings therefore have to be interpreted with caution. Secondly, a similar order effect as observed for the PSE was observed on the N1a peak. That is, participants who started with the motor prediction block showed more attenuation for congruent versus incongruent tones than participants who started with the non-motor prediction block. Unlike

perceptual attenuation, however, this effect was restricted to cue-based predictions.

The presence of the order effect on a neurophysiological level supports the previously proposed importance of learning history for sensory attenuation. The attenuation of the N1a peak itself is however hard to interpret as it does not coincide with previous work that has examined subcomponents of the N1 wave (Sanmiguel et al., 2013; Timm et al., 2013). In contrast to the present work, these previous studies only observed attenuation of the N1b and N1c peaks. Considering the exploratory nature of the current analyses, the above findings are therefore difficult to interpret.

The fact that we did not observe a generally reduced N1 amplitude for prediction-congruent versus prediction-incongruent tones was particularly surprising in case of the motor prediction condition. At first glance, this finding might seem to clash with previous demonstrations of neurophysiological attenuation following self- versus other-produced movements (Baess et al., 2011; Martikainen et al., 2005; Schafer and Marcus, 1973; Timm et al., 2013; Van Elk et al., 2014). It is important to note, however, that these studies examined the general influence of operational actions (i.e., actions that produce sounds) on sensory attenuation, whereas the present study scrutinized attenuation effects resulting from action-based predictions on the precise identity of a sound. The few existing studies that have hitherto examined such motor identity prediction effects have yielded mixed evidence (Baess et al., 2008; Bednark et al., 2015; Hughes et al., 2013b; Kühn et al., 2011).

The absence of clear identity-prediction effects in the current study also coincides with observations on other implicit measures of action-outcome perception, such as intentional binding. Similar to sensory attenuation, intentional binding (the temporal attraction of between self-produced actions and outcomes; Haggard et al., 2002) is generally attributed to motor predictive mechanisms (c.f., Moore and Haggard, 2008). However, studies directly comparing effects that are congruent or incongruent with action-based predictions have not found any evidence for this notion (Bednark et al., 2015; Desantis et al., 2012; Haering and Kiesel, 2014). This suggests that observed differences in perceptual processing of self-produced and externally produced effects are unlikely to be driven by specific motor-predictions as specified by forward models, but rather result from the more general heightened predictability of self-produced effects (Hughes et al., 2013a; Kaiser and Schütz-Bosbach, 2018). Taken together then, our results add to the existing evidence that both motor prediction and non-motor prediction effects on neurophysiological attenuation are not unequivocal and are possibly sensitive to variations in predictability manipulations across studies (see also Bednark et al., 2015).

4.3. Conclusions

Sensory attenuation is a fascinating phenomenon that is generally thought to play a pivotal role in our ability to distinguish the events that we cause ourselves from those that are caused by external sources. This proposition builds on the assumption that attenuation is particularly driven by specific *action-dependent* predictions about upcoming sensory input. The present study set out to examine this assumption by directly comparing attenuation of tones whose identity could be predicted from motor or non-motor sources. Overall only weak evidence for identity-prediction effects was observed. In fact, the only (small) attenuation effects that we observed were conditional upon participant's learning history within the task (i.e., effects were only present for participants who started with the motor prediction condition). At most, the current data therefore suggest that motor-prediction processes might facilitate causal learning. Importantly however, the underlying process of attenuation does not appear to be action-dependent. Specifically, the small observed perceptual attenuation effects were comparable for action-based and cue-based predictions, suggesting that attenuation is more likely to result from a more generic predictive mechanism.

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