



# Motor dominance and movement-outcome congruency influence the electrophysiological correlates of sensory attenuation for self-induced visual stimuli

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## ABSTRACT

This study explores the impact of movement-outcome congruency and motor dominance on the action-associated modulations of early visual event-related potentials (ERPs). Employing the contingent paradigm, participants with varying degrees of motor dominance were exposed to stimuli depicting left or right human hands in the corresponding visual hemifields. Stimuli were either passively observed or evoked by voluntary button-presses with the dominant or non-dominant hand, in a manner that was either congruent or incongruent with stimulus laterality and hemifield. Early occipital responses (C1 and P1 components) revealed modulations consistent with sensory attenuation (SA) for self-evoked stimuli. Our findings suggest that sensory attenuation during the initial stages of visual processing (C1 component) is a general phenomenon across all degrees of handedness and stimulus/movement combinations. However, the magnitude of C1 suppression was modulated by handedness and movement-stimulus congruency, reflecting stronger SA in right-handed participants for stimuli depicting the right hand, when elicited by actions of the corresponding hand, and measured above the contralateral occipital lobe. P1 modulation suggested concurrent but opposing influences of attention and sensory prediction, with more pronounced suppression following stimulus-congruent button-presses over the hemisphere contralateral to movement, especially in left-handed individuals. We suggest that effects of motor dominance on the degree of SA may stem from functional/anatomical asymmetries in the processing of body parts (C1) and attention networks (P1). Overall, our results demonstrate the modulating effect of hand dominance and movement-outcome congruency on SA, underscoring the need for deeper exploration of their interplay. Additional empirical evidence in this direction could substantiate a premotor account for action-associated modulation of early sensory processing in the visual domain.

## 1. Introduction

The sensory consequences of voluntary actions are processed differently than merely passively observed changes in the environment (Baess et al., 2011; Blakemore and Frith, 2003; Christoff et al., 2011; Haggard, 2005; Schröger et al., 2015). The neural background of this phenomenon has been explained by internal forward models, according to which, when preparing to perform an action, the motor system creates

an efference copy of the motor command that enables predicting the sensory effects of the movement in question. If these predictions match the outcome, corollary discharges in the relevant sensory cortices modulate the neural processing and perception of the sensory feedback (Blakemore et al., 2000; Wolpert et al., 1995; Wolpert and Miall, 1996). Through this mechanism, it has been postulated that agents are able to distinguish the consequences of their actions from external stimuli (Crape and Sommer, 2008). In humans, this process purportedly

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contributes to the sense of agency, i.e., the feeling of control over our own actions (Christoff et al., 2011; Moore and Haggard, 2008).

Numerous studies investigating the processing of self-generated stimuli in the auditory modality have reported that self-initiated sensory inputs are perceived as less intense than those generated externally (Desantis et al., 2012; Weiss et al., 2011a, 2011b). Such sensory attenuation (SA) effects have been corroborated by neurophysiological findings as well. Electroencephalography (EEG) has consistently revealed amplitude attenuation of the N1 event-related potential (ERP) to self-generated sounds (Baess et al., 2011; Bäss et al., 2008; Klaffehn et al., 2019; Lange, 2011; Martikainen et al., 2005; Mifsud et al., 2016; SanMiguel et al., 2013). Since the auditory N1 is sensitive to changes in sound intensity (Näätänen and Picton, 1987), i.e., louder sounds evoke a larger response, such N1 suppression to self-initiated sounds suggests that they are perceived as quieter relative to physically identical, but passively perceived control stimuli (Mifsud et al., 2016). Nevertheless, despite the mostly consistent findings, a handful of studies have reported no auditory SA, which the authors have related to the confounding effects of attention in their experimental setup (Chen et al., 2012; Ody et al., 2023; Paraskevoudi and SanMiguel, 2021; Reznik et al., 2014, 2015).

Results in the visual domain are fewer and less consistent, as studies have found both increased and reduced neural responses to self-initiated stimuli (Balla et al., 2019; Benazet et al., 2016; Buaron et al., 2020; Csifcsák et al., 2019; Gentsch and Schütz-Bosbach, 2011; Hughes and Waszak, 2011, 2014; Mifsud et al., 2016, 2018; Ody et al., 2023; Schafer and Marcus, 1973). The large variability of these findings is likely due to differences in the chosen paradigm, task and attentional demands, stimulus characteristics and timing. Furthermore, the selected electrode sites/regions of interest and investigated latencies also differ substantially, with no consensus on the nomenclature of the chosen components. The earliest ERP differences reported between self-initiated and passively encountered stimuli manifest already within 100 ms post-stimulus. Csifcsák et al. (2019) reported posterior C1 suppression to self-generated checkerboard and hand stimuli, while Ody et al. (2023) found an early N1<sup>1</sup> suppression in an intensity judgement task using abstract stimuli. SA effects were also detected at slightly later latencies in the form of anterior N1 attenuations (Gentsch and Schütz-Bosbach, 2011; Mifsud et al., 2018). The first findings that contradict the expected suppression effects well-established in the auditory modality were identified at a posterior positivity peaking between 100 and 150 ms post-stimulus. Modulation of this component, referred to as P1 or P2, was detected by a number of studies, both as an enhancement (Csifcsák et al., 2019; Hughes and Waszak, 2011), and as a suppression (Ody et al., 2023) to self-evoked visual stimuli. While a response enhancement may seem counterintuitive at first, it has been previously proposed that the modulation of this component may be affected by an interaction between SA and attention, stemming from the inherently unbalanced attentional demands of the traditional contingent paradigm (for a review, see Horváth, 2015). In particular, due to the higher predictability of self-initiated stimuli, their processing can be amplified by attention, which, depending on the behavioral paradigm, might counteract the neural correlates of SA and manifest in enhanced (rather than suppressed) ERPs (Balla et al., 2019; Csifcsák et al., 2019; Horváth, 2015; Hughes and Waszak, 2011). In support of this idea, our earlier study found smaller P1 enhancements for self-evoked stimuli (relative to passively viewing) when they were completely predictable, rather than being predictable only by onset timing, but not by configuration (Csifcsák et al., 2019). Since attentional demands were similar across conditions, we argued that smaller P1 amplitudes for completely predictable self-evoked stimuli reflect stronger SA, counteracting the effect of attentional enhancements (Csifcsák et al., 2019). Importantly, in their

recent study, Ody et al. (2023) controlled for such attentional bias by introducing involuntary button presses using an electromagnet. Their manipulation resulted in P2<sup>1</sup> suppression for self-generated versus externally generated stimuli, which is in line with the proposed interplay between SA and attention modulating this component (for similar findings in the auditory modality, see Timm et al., 2014). Lastly, the posterior visual N1 (or N145) ranging between 125 and 200 ms was also found to be either enhanced, unmodulated or attenuated for self-initiated (relative to passively viewed) images (Balla et al., 2019; Benazet et al., 2016; Csifcsák et al., 2019; Mifsud et al., 2016). The reasons behind these controversial findings are unclear, however, based on our earlier results from an experimental setup with higher ecological validity, we suggested that the posterior N1 may be sensitive to attentional amplification of domain-specific visual processes following voluntary actions (Balla et al., 2019).

Although it is known that neural processing of visual inputs shows category-specificity (e.g., Op de Beeck et al., 2010), there is scarce evidence on whether perceiving abstract (i.e., checkerboards) versus ecological stimuli, such as faces or hands, is encoded into internal forward models. The majority of visual experiments involved an experimental setup that does not reflect real-life situations, since they required performing simple hand movements to evoke abstract shapes (Benazet et al., 2016; Gentsch and Schütz-Bosbach, 2011; Hughes and Waszak, 2011; Mifsud et al., 2016; Ody et al., 2023). Previous findings, however, suggest that both ecological validity and the association or causal likelihood between the movement and its sensory consequence influence the predictions made by the motor system (Balla et al., 2019; Mifsud et al., 2018). Carrying out everyday movements, such as reaching for objects, is strongly associated with the sight of the corresponding hand in our visual field. Importantly, research suggests that the laterality of the perceived hand affects visual processing. For instance, we have previously reported larger P1 responses in the hemisphere contralateral to the identity of hand-stimuli (i.e., images of the left vs. right hand), despite central stimulus presentation (Csifcsák et al., 2019). Moreover, in a visual mismatch negativity (MMN) study, Stefanics and Czigler (2012) found that the laterality of the visually presented hand modulates the mismatch responses. Unexpected images of dominant right hands evoked more elaborate differential activity in the contralateral hemisphere than non-dominant left hands. From the perspective of the laterality of hands that trigger stimulus presentation, two previous functional magnetic resonance imaging (fMRI) studies have also shown that the laterality of the moving hand modulates neural responses to self-initiated visual (Buaron et al., 2020) and auditory (Reznik et al., 2014) stimuli.

While these findings point out that stimulus identity, movement laterality, and hand dominance may all affect action-associated neural processes, to our knowledge, no studies to date have systematically explored the role of these factors in SA. Given that all previous studies have involved only right-handed participants, it would be crucial to recruit individuals with a wider range of handedness scores (including left-handed and ambidextrous participants) to investigate if motor dominance and response-stimulus mappings influence early visual responses to self-initiated stimuli.

In the present study, we used the contingent paradigm involving voluntary button presses to trigger the presentation of stimuli depicting left- or right human hands to investigate how action-associated sensory modulations (as reflected by posterior ERPs) are affected by 1) the congruency between the laterality of movement and stimulus presentation, as well as 2) potential effects of motor dominance. Crucially, to enhance ecological validity between the laterality of the triggering movement and its sensory consequence, and also, to enable assessing hemisphere-specific ERP effects, hand stimuli were exclusively presented in their corresponding visual hemifields (i.e., a right hand in the right hemifield and vice versa), while participants were asked to maintain central fixation. We focused on three posterior visual ERP components, the C1, P1, and N1, and anticipated to replicate our

<sup>1</sup> Note that N1 and P2 in Ody et al. (2023) are at similar latencies and locations as C1 and P1 in Csifcsák et al. (2019).

previous findings (Csifcsák et al., 2019) regarding the attenuation of the C1 component and the enhancement of the P1 component for action-induced stimuli relative to passive viewing. We did not expect action-associated changes in the N1 amplitude, as previously we have only observed N1 modulation in a setting with higher ecological validity (Balla et al., 2019), but not for simple button presses (Csifcsák et al., 2019). Importantly, we hypothesized that the strongest amplitude reduction for the C1 and the weakest amplitude enhancement for the P1 following self-initiated stimulus presentation (both phenomena being indicative of SA) would occur 1) above the hemisphere contralateral to the stimulated hemifield, 2) above the hemisphere that is producing the efference copy (i.e., the left hemisphere for right-hand movements and vice versa), and 3) for stimuli and/or actions that are associated with the degree of motor dominance (i.e., left hand stimuli and/or left hand movements for strongly left-handed participants, and right hand stimuli and/or right hand movements for strongly right-handed participants), measured on a continuous scale (see Section 2.1).

## 2. Methods

### 2.1. Participants

Forty-three healthy adults participated in the experiment. Participants were recruited via university email lists and social media; they received 1500 HUF (approx. 5 EUR) as a compensation for their time. Data of 7 participants were excluded due to low signal-to-noise ratio or missing experimental conditions as a result of technical problems, hence, the final dataset consisted of data from 36 subjects (female: 22; age range: 18–36 years;  $M = 23.54$  years,  $SD = 4.15$ ). All participants had normal or corrected-to-normal vision, and based on self-report, none were diagnosed with psychiatric or neurological conditions. To assess handedness, we used the 20-item Edinburgh Handedness Inventory (EHI; Oldfield, 1971) to obtain the Laterality Index (LI) varying between scores of 100 (strong right-handedness) to  $-100$  (strong left-handedness). Based on the LI, 20 participants were right-handed (score  $> 48$ ), 11 participants were left-handed (score  $< -28$ ), and 5 were ambidextrous (score  $\geq -28$  but  $\leq 48$ ; overall range:  $-100$  to  $100$ ;  $M = 28.97$ ,  $SD = 68.84$ ). However, we note that LI scores were exclusively used as covariates in the statistical models, and we created groups based on handedness for data visualization purposes only. The study conformed with the Declaration of Helsinki and was approved by the Review Board of the Institute of Psychology, University of Szeged. All individuals provided signed informed consent and received no financial compensation for their participation.

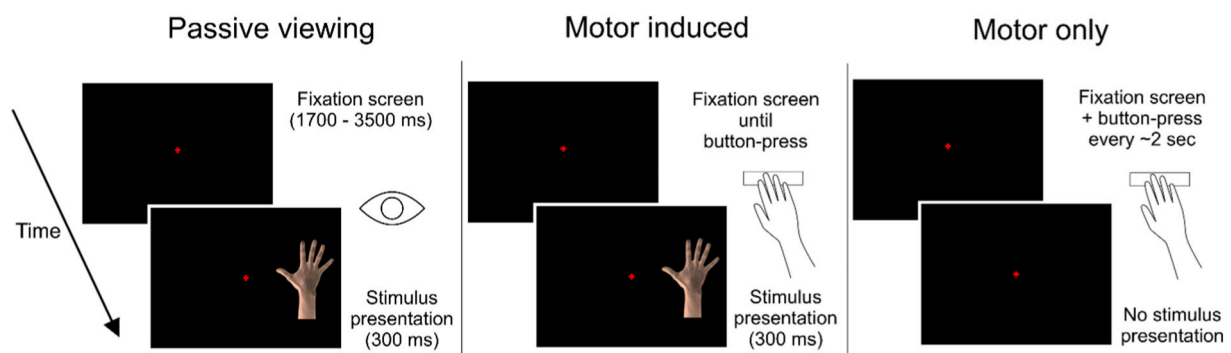
### 2.2. Stimuli and procedure

Data collection was performed in a dark, sound-attenuated room. Participants were seated in an armchair, 57 cm from a 20" LCD display

(LG Flatron; resolution:  $1024 \times 768$ ; refresh rate: 75 Hz; rectangular temporal window). Stimulus presentation was carried out using E-Prime 1.1 (Psychology Software Tools, Sharpsburg, PA). In each experimental condition, a red fixation cross (size:  $0.8^\circ$ ) was continuously present at the center of the screen. Stimuli consisted of computer-designed images depicting the dorsum of a right or left human hand and the distal one third of the forearm (size:  $10.5^\circ \times 12^\circ$ ; luminance:  $4.3 \text{ cd/m}^2$ ). The left-hand stimulus was the mirror image of the right-hand stimulus. Hand stimuli were presented over a black background, the medial edge of the hand was presented  $4.5^\circ$  from the center of the screen.

We adapted the contingent paradigm, which typically consists of three main experimental conditions (Fig. 1): passive viewing (PV), motor induced (MI), and motor only (MO). During PV, participants were instructed to maintain fixation, while stimuli appeared peripherally for 300 ms with a randomized interstimulus interval (ISI) of 1700–3500 ms for 100 repetitions, resulting in a median ISI of 2600 ms in each condition. We included two different PV blocks: PV-RH involved right-hand stimuli presented in the right hemifield, while PV-LH involved left-hand stimuli presented in the left hemifield. In the MI condition, participants were asked to press the response key in a self-paced manner, while maintaining fixation. Each button-press triggered immediate stimulus presentation for 300 ms. Participants were instructed to keep their fingers on the response button continuously and to avoid unnecessary movements. They were asked to aim at an approximately 2 s pace (without counting the elapsed time) and were told that the software would not respond to much faster button-presses (no stimulus was presented below 1500 ms since the previous button-press). We included four MI blocks, each involving 100 trials: in the MI-RH-RM and MI-RH-LM blocks, right-hand stimuli were presented in the right hemifield as a result of right- or left-hand movements (hence RM or LM), while in the MI-LH-RM and MI-LH-LM blocks, left-hand stimuli were presented in the left hemifield as a result of right- or left-hand movements, respectively. In the MO conditions, participants performed self-paced button-presses after receiving the same instructions as in the MI blocks. No stimuli were presented after the button-presses, however, participants were asked to maintain fixation centrally during all 100 trials. Each subject performed two MO blocks: in the MO-RM block they used their right hand, while in the MO-LM block they used their left hand. Each MI and MO block started with a 10-trial-long practice session, during which participants received immediate feedback about their response times to get acquainted with the required pace. EEG markers were synchronized to the stimulus presentation in PV and MI blocks, and to the screen immediately following a button press in MO blocks, where stimulus presentation was absent.

Overall, the study consisted of 8 blocks, each containing 100 trials: PV-RH, PV-LH, MI-RH-RM, MI-RH-LM, MI-LH-RM, MI-LH-LM, MO-RM, and MO-LM. The order of the blocks was counterbalanced across participants. The mean duration of PV blocks was 4.8 min, while MI and MO blocks lasted for approximately 5–7 min, depending on individual



**Fig. 1.** Overview of the main conditions of the paradigm. In the passive viewing (PV) and motor induced (MI) conditions, identical visual stimuli were presented, while the MI and motor only (MO) conditions included identical motor requirements.

response times. Participants were required to take at least a 10 min break halfway through the experiment, during which the handedness test was administered. Additionally, they had the possibility to take a short break between the blocks as well. Four additional blocks (two PV blocks: left hand stimuli presented in the right hemifield, and right-hand stimuli presented in the left hemifield, and two MI blocks: left hand stimuli presented in the right hemifield, elicited by right hand movements, and right-hand stimuli presented in the left hemifield, elicited by right hand movements) were also performed during the experiment, which are not analyzed in the present study. Including all 12 recorded blocks, the duration of the task was approximately 70 min, while the full experimental session, including preparation time, lasted for about 2 h.

### 2.3. EEG recording and analysis

EEG was recorded with a BioSemi ActiveTwo Amplifier (BioSemi, Amsterdam, The Netherlands) at a 1024 Hz sampling rate, using 32 scalp Ag/AgCl electrodes placed according to the extended international 10/20 system (at positions Fp1, Fp2, AF3, AF4, F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, PO3, PO4, O1, Oz, O2). Eyeblink artifacts were monitored at the Fp1 and Fp2 electrodes, and horizontal eye movements were monitored at the F7 and F8 electrodes. The recording reference and the ground electrodes (common mode sense and driven right leg electrodes in the ActiveTwo system, [Metting van Rijn et al., 1990](#)) were placed close to the Cz position. Data were recorded without applying frequency filters.

To successfully achieve lateral stimulus presentation, it was essential that participants maintain fixation to the centrally presented fixation stimulus and avoid blinking, as much as possible, during stimulus presentation throughout all experimental blocks. To ensure that these criteria are met and no unwanted eye movements during stimulus presentation remain in the final dataset, we marked all data points where horizontal eye movements or eyeblinks were present using BrainVision Analyzer (Brain Products GmbH, Gilching, Germany). To this end, after filtering the data between 1 Hz and 5 Hz, two new channels, VEOG and HEOG were created. For the VEOG channel, the Fp1 and Fp2 channels were averaged together, then, to amplify low-amplitude blink artifacts, it was multiplied by 3. Two new markers were placed to every eyeblink artifact: the first one to the time point where it passed a +100  $\mu\text{V}$  threshold, and the second one to its peak. For the HEOG channel, we multiplied the F7 and F8 channels together to increase signal-to-noise ratio and placed markers to every lateral eye movement at time points where they passed a -300  $\mu\text{V}$  threshold and to their peak. These new markers were then imported into their respective raw data files in the EEGlab toolbox ([Delorme and Makeig, 2004](#)) for Matlab (MathWorks, Natick, MA), where all remaining preprocessing steps were carried out. We first applied a 1 Hz high-pass filter to the raw EEG data, then removed line noise using the cleanLineNoise function from the PREP pipeline ([Bigdely-Shamlo et al., 2015](#)). Next, we used the clean\_rawdata plugin to correct continuous data using Artifact Subspace Reconstruction (ASR) ([Kothe and Makeig, 2013](#)), as well as to identify and reject bad channels, which were then interpolated. Epochs including 100 ms pre- and 600 ms post-stimulus were extracted using ERPLab ([Lopez-Calderon and Luck, 2014](#)). To prevent the exclusion of (and instead only clean) epochs containing eyeblink artifacts solely after stimulus presentation, we conducted independent component analysis (ICA). To achieve better decomposition, ICA was performed on a more aggressively cleaned average-referenced copy of the dataset that was down-sampled to 250 Hz and low-pass filtered at 45 Hz. The ICA weight matrix was then applied to the original dataset, after which baseline removal was performed -100 ms - 0 ms relative to stimulus presentation. ICA components corresponding to ocular artifacts were classified and removed using the ICLabel function ([Pion-Tonachini et al., 2019](#)). Finally, data were re-referenced to Fz and all remaining epochs that contained any of the previously marked eyeblink or lateral eye movement markers (indicating that the subject blinked or looked away from

the fixation stimulus) during or right before stimulus presentation (-100 ms to 300 ms) were rejected. Preprocessing yielded on average 92.52 trials (SD = 9.15) per condition, indicating that in the majority of trials, participants maintained fixation during the critical time interval of stimulus presentation (or the lack thereof in MO-trials). Epochs corresponding to each experimental block were averaged using ERPLab. ERPs obtained in the MO-RM and MO-LM blocks, containing neural activity related to motor preparation and execution, were subtracted from the corresponding MI data of the same participant (MI-RH-RM - MO-RM, MI-RH-LM - MO-LM, MI-LH-RM - MO-RM, MI-LH-LM - MO-LM), resulting in the following "corrected motor induced" (CMI) difference waveforms: CMI-RH-RM, CMI-RH-LM, CMI-LH-RM, CMI-LH-LM. Thus, we were able to compare PV and CMI data directly to assess changes in visual processing. Mean C1, P1, and N1 amplitudes centered around peaks identified in the grand average waveform of all participants and PV conditions were extracted at posterior channels (C1, P1: O1/O2, N1: P7/P8) in the 95-115 ms, 135-175 ms, and 180-220 ms time windows, respectively (Supplementary Fig. 1).

### 2.4. Statistical analysis

Repeated-measures analysis of variance (rmANOVA) models were fitted to data using JASP 0.18 ([JASP Team, 2023](#)), whereas linear mixed-effects analysis was performed using the *lmer* function of the *lme4* package in R ([R Core Team, 2021](#)).

#### 2.4.1. Pacing speed data

Pacing speed (PS) data was compared between MO and MI conditions to verify that participants maintained a similar pace of responding in these blocks. In addition, we also assessed if PSs corresponding to responses with the right vs. left hand were different, while controlling for handedness-scores. Median PSs were calculated for each participant and condition (MI-RM, MI-LM, MO-RM, MO-LM), irrespective of stimulus type (merged across RH and LH) and entered as dependent variables in a rmANOVA with CONDITION (MI vs. MO), HAND (RM vs. LM) as within-subject factors and HANDEDNESS (LI scores) as covariate. Effects were considered as significant at  $p < .05$ , estimates of effect size ( $\eta_p^2$ ) are also provided.

#### 2.4.2. ERP data

First, we assessed if action-associated modulations of C1, P1 and N1 amplitudes were present in our dataset, irrespective of stimulus type (RH or LH) and laterality of movement (RM or LM). Therefore, mean ERP amplitudes for the PV and CMI conditions were calculated after collapsing across these factors, and separate rmANOVAs were performed for each ERP component with CONDITION (PV vs. CMI) and ELECTRODE (C1 and P1: O1 vs. O2; N1: P7 vs. P8) as within-subject factors. Single electrodes were chosen to quantify the components in order to maintain comparability with our previous studies ([Balla et al., 2019](#); [Csifcsák et al., 2019](#)). To detect potential effect of handedness on ERP lateralization, we also added HANDEDNESS as covariate.

Next, we focused on our main research question and investigated whether action-associated ERP modulations were sensitive to stimulus type, movement laterality and/or handedness. For this analysis, mean C1, P1 and N1 amplitudes were measured on the PV - CMI difference waveforms and entered into rmANOVAs as dependent variables, with STIMULUS (RH vs. LH), congruence of MOVEMENT relative to the visual stimulus (congruent: RM for RH, LM for LH stimuli; incongruent: RM for LH, LM for RH stimuli) and HEMISPHERE relative to the side of stimulus presentation (ipsilateral: O1/P7 for LH, O2/P8 for RH stimuli; contralateral: O1/P7 for RH, O2/P8 for LH stimuli) as within-subject factors, as well as HANDEDNESS score as covariate. To reduce dimensionality of the data, significant ( $p < .05$ ) three-way or four-way interactions were followed-up with linear mixed-effects models with difference scores (hemisphere effects: ipsilateral - contralateral; movement effects: incongruent - congruent; stimulus effects: LH - RH) as

dependent variables, the remaining factors as fixed-effects and by-participant random intercepts and slopes.

### 3. Results

#### 3.1. Pacing speed

Pacing speed was faster in MI relative to MO conditions ( $F(1,34) = 76.57, p < .001, \eta_p^2 = 0.692$ ; MI:  $M = 2625.6$  ms,  $SD = 488.1$ , MO:  $M = 2906.8$  ms,  $SD = 449.0$ ), but this effect was not modulated by the laterality of movement and/or handedness ( $p > .57$ , Supplementary table 1). Neither of the other main effects were significant ( $p > .384$ , Supplementary table 1).

#### 3.2. ERPs

Grand average ERPs across PV and CMI conditions for each stimulus type (RH and LH) showed lateralized posterior activity with respect to the visual hemifield of stimulus presentation, supporting the reliability of the EEG processing in restricting the analysis to epochs where participants maintained central fixation (Fig. 2, for a more detailed time resolution, see Supplementary Fig. 3). Waveforms from all experimental conditions are presented in Fig. 3, separately for right-handed vs. ambidextrous/left-handed participants.

##### 3.2.1. The C1 component

We found a significant action-associated reduction of the occipital C1 relative to passive viewing irrespective of stimulus type and the congruence of the eliciting movement (CONDITION:  $F(1,34) = 27.27, p < .001, \eta_p^2 = 0.45$ ). While the main effect of ELECTRODE, the CONDITION  $\times$  ELECTRODE, CONDITION  $\times$  HANDEDNESS and CONDITION  $\times$  ELECTRODE  $\times$  HANDEDNESS interactions were not significant ( $p > .103$ ; Supplementary Table 2), lateralization of the C1 amplitude was significantly modulated by handedness of the participants (ELECTRODE  $\times$  HANDEDNESS:  $F(1,34) = 6.54, p = .015, \eta_p^2 = 0.16$ ). This surprising results was followed up post-hoc with Pearson's correlation, which revealed a significant negative association between the lateralization of the C1 amplitude (O1 – O2 difference amplitudes) and handedness scores ( $r(34) = -0.402, p = .015$ ), indicating that the C1 was larger above the motor-dominant hemisphere of participants (i.e., more prominent right-handedness was associated with larger C1 components above the left hemisphere; Supplementary Fig. 2).

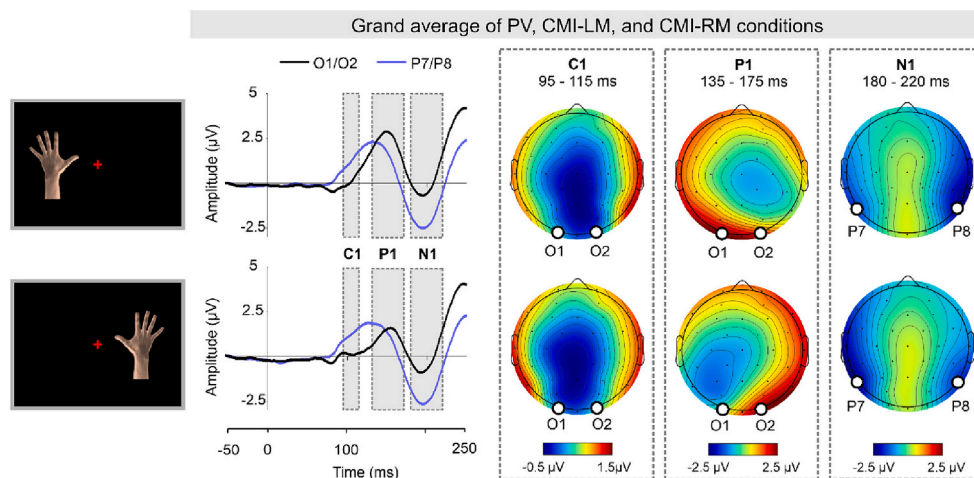
Analysis of the PV – CMI difference waveforms revealed no significant main effects or interactions ( $p > .149$  for all; Supplementary

Table 3) except for a significant 4-way STIMULUS  $\times$  MOVEMENT  $\times$  HEMISPHERE  $\times$  HANDEDNESS interaction ( $F(1,34) = 7.41, p = .010, \eta_p^2 = 0.18$ ). To follow-up on this effect, C1 amplitude differences for STIMULUS were calculated (LH – RH, so that more positive values indicate larger action-related C1 reduction for RH relative to LH stimuli) and fitted a linear mixed-effects model with HANDEDNESS, MOVEMENT (0: incongruent, 1: congruent) and HEMISPHERE (0: ipsilateral, 1: contralateral) as fixed effects (model C1–1). Following the same logic, similar linear mixed-effects models were fitted to C1 difference amplitudes for MOVEMENT (incongruent – congruent, so that more positive values represent larger movement-related C1 reduction for congruent relative to incongruent movements; model C1–2), and HEMISPHERE (ipsilateral - contralateral, so that more positive values represent larger C1 reduction in CMI waveforms at electrodes contralateral to the hemifield of visual presentation; model C1–3). In these latter two models, STIMULUS (0: LH, 1: RH) replaced MOVEMENT or HEMISPHERE as fixed factors, respectively. All three models revealed significant three-way interactions between HANDEDNESS and the other two factors, while none of the main effects or two-way interactions were significant (see Supplementary Table 4). Importantly, the coefficient for the three-way interaction was positive ( $b = 0.014, 95\% \text{ CI} = [0.004, 0.024], t(34) = 2.72, p = .010$ ), indicating that action-associated reduction of the C1 amplitude was increased 1) for RH stimuli, 2) following stimulus-congruent movements, 3) above the occipital hemisphere contralateral to stimulus presentation, and 4) with the degree of right-handedness (Fig. 4a; see also Supplementary Fig. 4).

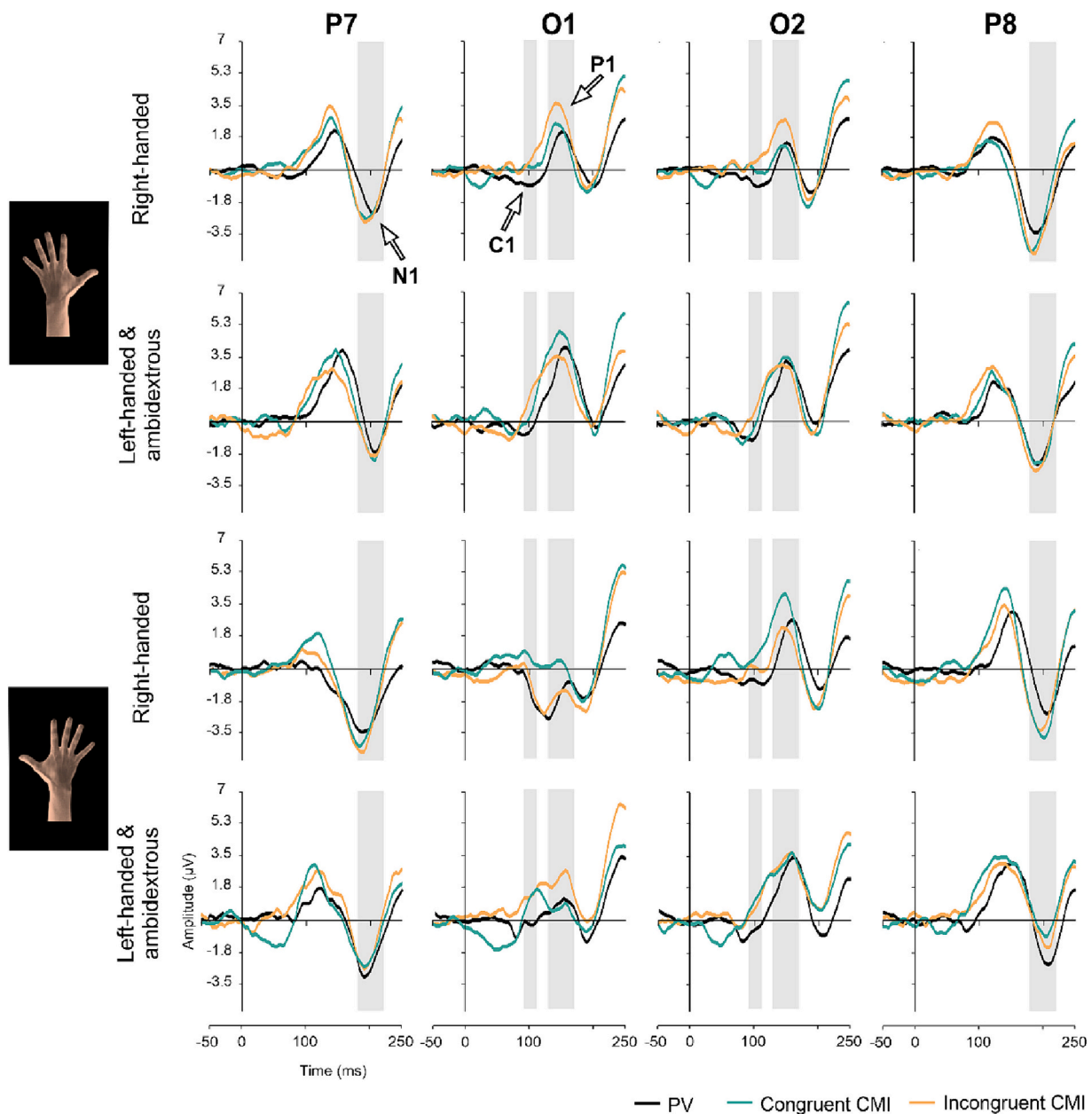
##### 3.2.2. The P1 component

With respect to movement-related modulations of the occipital P1 component, we found no evidence for an overall effect ( $p > .250$ , Supplementary Table 5). The model revealed a significant main effect of ELECTRODE, indicating larger P1 amplitudes above the right relative to the left occipital lobe (electrode O2 vs. O1;  $F(1,34) = 7.68, p = .009, \eta_p^2 = 0.18$ ), independent of handedness scores ( $p = .224$ , Supplementary Table 5).

The PV – CMI difference waveforms were negative for all conditions, except for LH stimuli elicited by stimulus-congruent movements, measured above the contralateral hemisphere, and for RH stimuli elicited by stimulus-incongruent movements, measured above the ipsilateral hemisphere (Supplementary Table 6). In other words, the two conditions with action-related P1 amplitude reduction instead of enhancement were those where participants had to use their left hands to initiate stimulus presentation, and the P1 was quantified above the hemisphere contralateral to the side of the movement (Fig. 5).



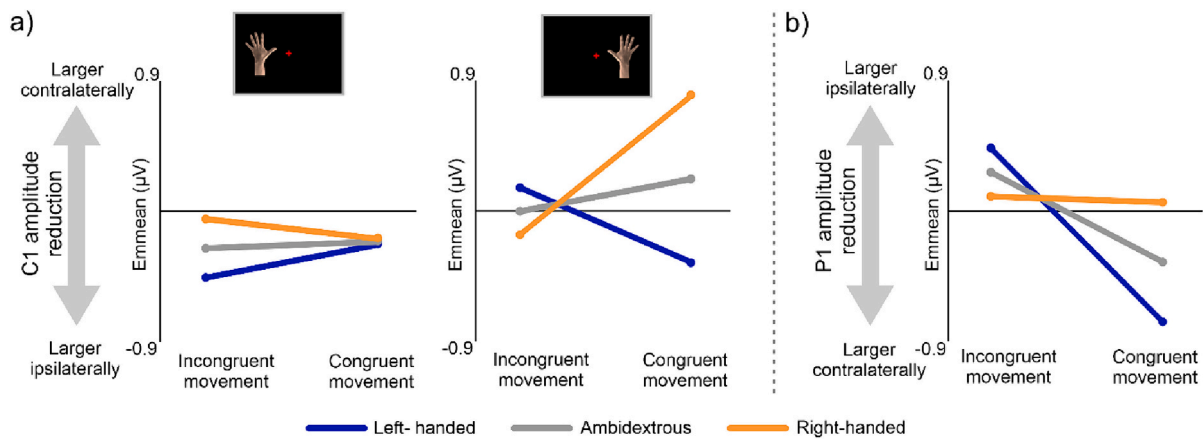
**Fig. 2.** Grand average ERPs across passive viewing (PV) and corrected motor induced (CMI) conditions performed with left- (LM) and right-hand (RM) movements, separated by stimulus type (LH: upper row, RH: lower row), at the average of O1 & O2, and P7 & P8 electrodes. Average scalp maps from the 3 investigated time-windows (marked with grey rectangles) show lateralized posterior activity depending on the visual hemifield of stimulus presentation.



**Fig. 3.** ERPs at four posterior electrodes for left- and right-hand stimuli, separately for right-handed and ambidextrous/left-handed participants. PV = passive viewing condition, Congruent CMI = corrected motor-induced condition where the laterality of the stimulus-triggering hand aligns with stimulus laterality and hemifield, Incongruent CMI = corrected motor-induced condition where the stimulus-triggering hand is contralateral to stimulus laterality and hemifield.

Statistical analysis of the PV – CMI difference waveforms showed significant MOVEMENT  $\times$  HEMISPHERE interaction ( $F(1,34) = 9.14$ ,  $p = .005$ ,  $\eta_p^2 = 0.21$ ), with weaker P1 enhancement for self-induced vs. passively viewed stimuli above the hemisphere contralateral to stimulus presentation for stimulus-congruent movements, and above the ipsilateral occipital region for stimulus-incongruent movements (Fig. 6). This pattern was indicative of a significantly smaller P1 amplitude change at electrodes contralateral relative to the hand that produced the button presses (i.e., O1 and O2 for right- and left-hand actions, respectively). However, the MOVEMENT  $\times$  HEMISPHERE  $\times$  HANDEDNESS interaction was also significant ( $F(1,34) = 4.82$ ,  $p = .035$ ,  $\eta_p^2 = 0.12$ ), while main effects and other interactions were below significance level ( $p > .05$  for all; Supplementary Table 7). The significant three-way interaction was followed-up with two separate linear mixed-effects model, one with the HEMISPHERE effect (ipsilateral – contralateral difference, with more negative values representing weaker action-associated P1

increase above the hemisphere contralateral to stimulus presentation; model P1-1) and one with the MOVEMENT effect (incongruent – congruent difference, with more negative values indicating weaker P1 enhancement following movements that are congruent with the presented stimulus; model P1-2) as dependent variable, while HANDEDNESS and the other variable (MOVEMENT and HEMISPHERE, respectively) were entered as fixed factors. In model P1-1, the estimate for the coefficient for MOVEMENT was significant, with a negative value pointing at less pronounced P1 increase above the contralateral hemisphere following stimulus-congruent movements ( $b = -0.086$ , 95 % CI =  $[-1.422, -0.303]$ ,  $t(34) = -3.02$ ,  $p = .005$ ). However, this effect was counterbalanced by HANDEDNESS, reflected by a significant positive coefficient for the interaction term ( $b = 0.009$ , 95 % CI =  $[0.001, 0.016]$ ,  $t(34) = 2.20$ ,  $p = .035$ ), so that the effect of movement congruence on the ipsi- vs. contralateral difference was weaker with increasing degree of right-handedness (i.e., the effect was stronger in left-handed



**Fig. 4.** The influence of motor dominance on the degree of action-associated amplitude suppression of the C1 (a) and P1 (b) components, from statistical models C1-3 and P1-1, respectively. a) Difference in action-associated C1 amplitude reduction over the hemisphere ipsi- vs. contralateral to stimulus presentation, separated by stimulus type and movement-stimulus congruency for each handedness group. More positive values indicate larger C1 amplitude suppression over the contralateral hemisphere, while more negative values indicate larger C1 amplitude suppression over the ipsilateral hemisphere; b) Difference in action-associated P1 amplitude reduction over the hemisphere ipsi- vs. contralateral to stimulus presentation, separated by movement-stimulus congruency for each handedness-group. More positive values indicate larger P1 amplitude suppression over the ipsilateral hemisphere, while more negative values indicate larger P1 amplitude suppression over the contralateral hemisphere. Emmean = Estimated marginal mean.

participants; Fig. 4b). Conceptually similar effects were found for model P1-2, whereby action-associated P1 increase of smaller magnitude was found for congruent vs. incongruent movements above the contralateral hemisphere, but this effect was less pronounced for participants with stronger degree of right-handedness (Supplementary Table 8).

### 3.2.3. The N1 component

Finally, analysis of the occipitotemporal N1 did not reveal any significant effects ( $F < 2.58$ ,  $p > .117$  for all; Supplementary table 9), suggesting that no systematic action-associated amplitude modulation was present for this component. Analysis of the PV – CMI waveforms yielded similar results, with no significant effect of stimulus type, movement congruence, hemisphere of N1 measurement or handedness of participants regarding this ERP component ( $F < 3.00$ ,  $p > .092$  for all; Supplementary table 10).

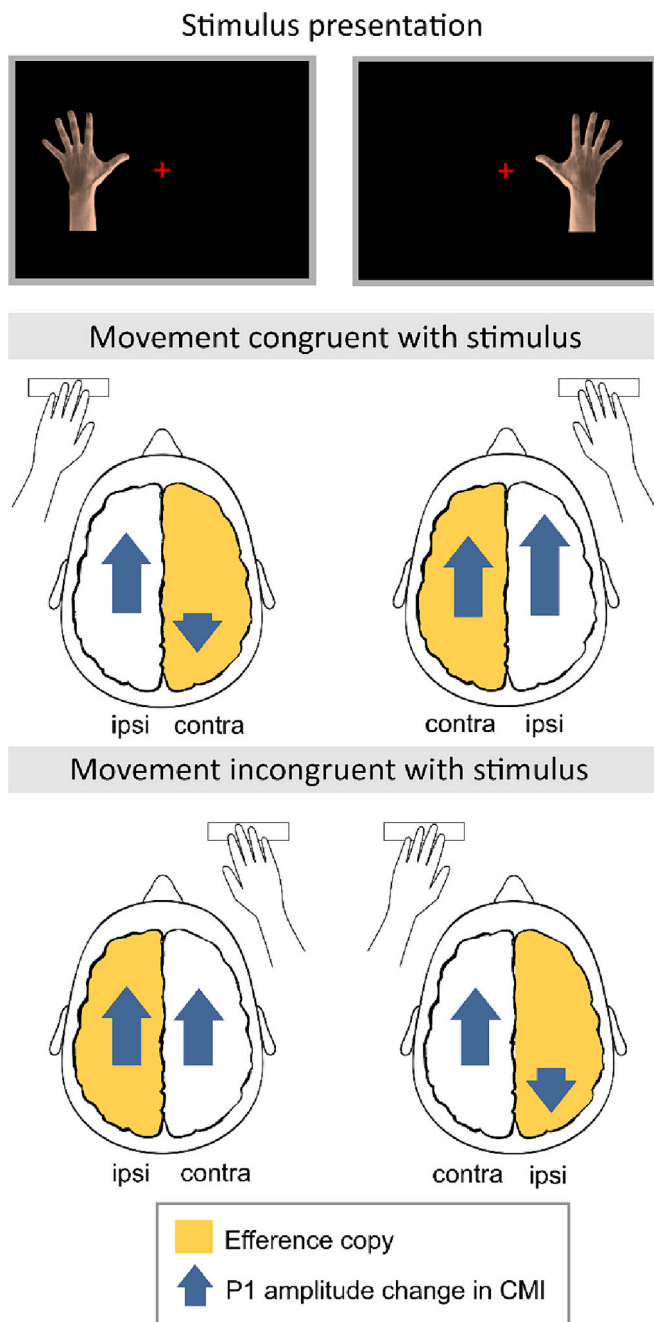
## 4. Discussion

The aim of the present study was to examine how modulations of visual processing triggered by voluntary actions are affected by the congruency between movement and stimulus presentation, as well as hand dominance. To expand upon previous studies that solely examined right-handed participants, we also involved left-handed and ambidextrous individuals in our experiment. Using the contingent paradigm, we presented visual stimuli depicting left or right human hands in the corresponding visual hemifield to participants with a wide range of handedness scores. Stimulus presentation was either passively observed or evoked by voluntary button-presses performed either with the dominant or the non-dominant hand, in a manner that was either congruent or incongruent with the laterality of the hand stimulus and stimulated hemifield. We investigated the modulation of three early posterior ERP components, the C1, P1 and N1, and found evidence for overall C1, and in certain conditions P1 modulation, both indicating sensory attenuation. These effects were influenced by stimulus identity (for the C1), as well as motor dominance and movement congruency (for both the C1 and P1 components). However, we found no evidence whatsoever for action-associated modulation of the N1 component with this paradigm.

### 4.1. Sensory attenuation affects early occipital responses to self-evoked visual stimuli

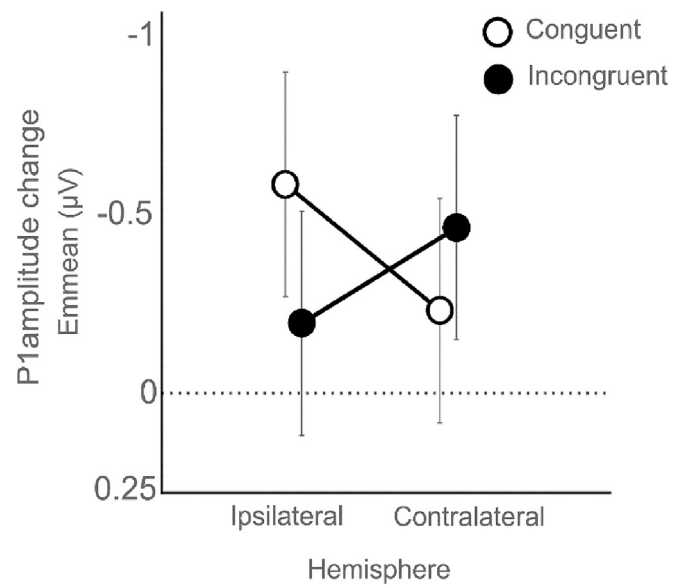
In line with our expectation, we identified an overall action-associated suppression of the C1 component compared to passive viewing, following both congruent, and incongruent movements, regardless of stimulus type or motor dominance. This result further corroborates the conclusions of several previous studies that also reported SA already at such an early stage of visual processing to both abstract (Csifcsák et al., 2019; Ody et al., 2023) and ecological stimuli (Csifcsák et al., 2019), pointing at a very elementary (and possibly automatic) process in the chain of sensory processing. Despite earlier studies arguing that the C1, purportedly generated in the primary visual cortex, is insensitive to attentional modulation (Fu et al., 2010; Hillyard and Anllo-Vento, 1998), more recent results have challenged this view. In a recent systematic review and meta-analysis, Qin et al. (2022) found that attention has a moderate effect on the C1, with its amplitude being larger for attended compared to non-attended visual stimuli. Consequently, even if the attentional imbalance between the conditions of the contingent paradigm affected the C1, it cannot account for its suppression since attention would theoretically enhance its amplitude. Thus, our finding likely reflects efference copy-based predictive processes 95–115 ms post-stimulus presentation, leading to altered processing of the outcomes of self-initiated actions (Schröger et al., 2015, but see: Kaiser and Schütz-Bosbach, 2018).

The P1 amplitude was not globally modulated by the presence or absence of movements triggering stimulus presentation, which may be due to attention and prediction simultaneously influencing this component in an opposing manner in the CMI condition. Since we expected that stronger attentional orientation to self-produced stimuli would amplify the P1, while predictive processes would counteract this effect by causing SA, we hypothesized that smaller P1 enhancements (or larger P1 reductions) will be indicative of sensory attenuation outweighing attentional amplification (Csifcsák et al., 2019; Hughes and Waszak, 2011), and such effects would depend on movement congruence, stimulus type and/or hemispheric lateralization. In line with this, while the P1 numerically increased for action-associated stimulus presentation in most conditions (reflecting a prominent role of attentional amplification), our analysis also revealed that the magnitude of P1 modulation varied across experimental conditions. Specifically, we identified significantly smaller P1 enhancement above the hemisphere contralateral to the side of movement, effectively manifesting in SA



**Fig. 5.** Relative proportion of P1 amplitude change (blue arrows) in the corrected motor induced (CMI) condition, over the ipsi- and contralateral hemispheres (relative to stimulus presentation) for stimulus-congruent and incongruent movements, separated by stimulus type (LH stimuli: left column; RH stimuli: right column). The yellow shading marks the hemisphere where the motor command and the efference copy are generated. Emmean = Estimated marginal mean. Error bars depict the 95 % confidence interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

following button-presses executed with the left hand (see Figs. 5 & 6). Such a hemispheric lateralization effect supports the notion that predictive processes counteract the attention-related P1 enhancement, as they were restricted to the hemisphere that controls the movement and purportedly produces the efference copy that leads to corollary discharges in sensory areas (Schröger et al., 2015; Wolpert and Miall, 1996). A putative explanation for why SA was only observed for left-hand button presses may be related to the lateralization of attentional



**Fig. 6.** P1 amplitude change (passive viewing – corrected motor induced difference) for stimulus-congruent and incongruent movements over the ipsi- and contralateral hemispheres (relative to stimulus presentation). Emmean = Estimated marginal mean. Error bars depict the standard error. Negative values are plotted up.

networks as a function of motor dominance (i.e., the degree of handedness), and will be discussed in Section 4.2.

Finally, our analysis revealed no notable N1 amplitude modulation to self-evoked stimuli in any of the experimental conditions, replicating our previous findings with a similar paradigm involving simple button-presses (Csifcsák et al., 2019). As we previously argued, the action-associated modulation of intermediate-level visual processing reflected by the posterior N1 is likely sensitive not only to the category of the stimulus, but also to the context in which it is presented (Balla et al., 2019). In our earlier study with improved ecological validity relative to the current paradigm as well as a reinforced association between movements and their visual outcomes, we identified a significant N1 enhancement, supporting the notion that the posterior N1 is expected to be modulated only in a setting with a stronger association and sense of control over the presented stimulus (Balla et al., 2019).

#### 4.2. Hand dominance modulates occipital action-associated predictive processes

We found that both the C1 and P1 components were significantly affected by hand dominance, and for the occipital C1, we also identified movement-independent effects. Namely, our results showed that the degree of C1 lateralization correlated with participants' handedness, being larger above the motor-dominant hemisphere both in the PV and in CMI conditions, regardless of the laterality of the stimulus (Supplementary Fig. 2). This result indicates that motor dominance already affects the lateralization of the earliest stages of visual processing.

With respect to the main aims of the current study, we also observed that the suppression of the C1 component to self-induced stimuli was significantly modulated by an interaction between stimulus identity, movement congruency, the hemisphere of measurement and handedness. Specifically, higher degree of right-handedness was associated with stronger C1 suppression for right-hand stimuli above the contralateral (left) hemisphere, if stimulus onset was controlled via actions performed with the dominant (and stimulus-congruent) hand (Fig. 4a).

A perceptual bias toward the dominant hand has been identified in visual studies involving participants with varied degrees of handedness. In a visual discrimination task involving speeded left-right judgements



about a schematic human figure, [Gardner and Potts \(2010\)](#) reported a right hemifield bias for right-handed and ambidextrous participants, and a left hemifield bias for left-handed participants. The authors interpreted this results in the context of the premotor theory of attention, proposing that stimulus processing is facilitated by a stronger “readiness to act” in the space toward which a motor command is prepared. Similarly, [Pierce et al. \(1996\)](#) found that participants responded faster to stimuli in the hemifield of their dominant hand. Thus, we propose that our result regarding the C1 component could be explained by an inherent bias in perceptual-predictive processes based on motor dominance, modulating the readiness for perceptual analysis of the consequences of upcoming actions (the “premotor theory of action-associated sensory predictions”).

Surprisingly, however, we did not find a similar bias toward the dominant hand in the left-handed group. A similar bias would have manifested as a more pronounced C1 suppression for LH stimuli above the contralateral (right) hemisphere during stimulus-congruent dominant-hand movements, but instead, this effect was larger ipsilaterally for both left- and right-hand movements (see [Fig. 4a](#)). This result could be explained by the high prevalence of right-handedness in the population, due to which, images of right hands may be similarly relevant for left-handed individuals, as those depicting their dominant left hand ([Marzoli et al., 2014](#)). Another plausible explanation for this finding could be rooted in variations in the cortical lateralization of visual processing among right- and left-handed individuals. For instance, in an fMRI study, [Willems et al. \(2010\)](#) showed that the extrastriate body area (EBA) is right-lateralized in right-handers, while no hemispheric lateralization is present in left-handers. While our results do not entirely align with this observation - given that we observed a greater C1 suppression above the left hemisphere rather than the right - we can still underscore that the processing bias for body parts presented in the right versus left hemifield appears more pronounced in right-handed individuals. Thus, the interaction which reflects that SA of the C1 was the largest for RH stimuli evoked by dominant right-hand actions above the contralateral hemisphere, may be attributed to stronger anatomical asymmetry in the neural representation of hands linked to right-handedness, a distinction not observed in left-handed participants.

Regarding the P1, we have also found evidence that movement-associated amplitude modulation of this component is affected by the degree of motor dominance. We identified that P1 enhancement following button presses was weaker in the hemisphere contralateral to the side of movement, being indicative of the influence of prediction-related P1 suppression (see [Fig. 6](#)). Interestingly, this effect was especially prominent in left-handed individuals, and conversely, P1 modulation was largely similar across the two hemispheres in strongly right-handed participants (see [Fig. 4b](#)). Given the sensitivity of the P1 to visual attention ([Correa et al., 2006](#); [Hughes and Waszak, 2011](#)), this finding may be explained by variations in the lateralization of attentional networks with hand dominances. For instance, the dorsal attention network (DAN) was proposed to be strongly right-lateralized in left-handed individuals, with no such lateralization associated with right-handedness ([Petit et al., 2015](#)). The absence of P1 suppression in right-handers may therefore be attributed to the more bilateral organization of the DAN. Consequently, prediction-based P1 attenuation in right-handers, which, for left-hand movements should generate an efference copy in the right hemisphere, might possibly not effectively counteract the effect of attentional amplification, since it could in principle also arise from left DAN activity. In left-handers, however, both attentional and predictive influences are more restricted to the same (right) hemisphere, resulting in a stronger interaction effect and a consequential action-associated P1 suppression.

It is important to mention that the observed C1 and P1 modulations associated with handedness do not entirely align with our initial predictions. For the C1 component, we also anticipated SA for LH stimuli following congruent movements in left-handers, and similarly, we expected P1 reduction for right-lateralized movements in right-handed

participants as well. We emphasize therefore that the explanations put forth to interpret our findings are post hoc in nature. Regarding the C1 suppression, it's worth noting that not all studies have consistently observed a leftward visual bias dependent on handedness (e.g., [Smigajewicz et al., 2017](#)). Concerning the effect that we identified for the P1, [Petit et al. \(2015\)](#) also discuss several studies that have not demonstrated a significant influence of manual preference on the right-lateralization of the DAN (e.g., [Badzakova-Trajkov et al., 2010](#); [Powell et al., 2012](#)). Nevertheless, our findings highlight the impact of motor dominance/handedness on action-associated modulations of early occipital visual responses - an aspect largely overlooked in current research on the electrophysiological correlates of SA. Therefore, even studies exclusively involving right-handed participants may fail to account for subtle variations in handedness, potentially omitting a crucial factor influencing their findings. We believe that a more comprehensive exploration that includes left-handed and ambidextrous participants is warranted to capture a fuller understanding of the effects of hand dominance on SA, and whether a premotor account for action-associated modulation of visual processing can be supported by accumulating empirical evidence.

#### 4.3. Congruency between movement and its visual outcome leads to stronger sensory attenuation

Both the C1 and P1 component exhibited greater SA in cases when the stimulus-triggering movement was congruent with the presented visual outcome, that is, when the identity of the hand stimulus and the stimulated hemifield coincided with the participant's moving hand. The concept of congruency, or the degree of stimulus-movement association, can be approached from various perspectives, as explored by a handful of previous studies. [Mifsud et al. \(2016, 2018\)](#) conducted two experiments, investigating SA for auditory (Study 1) and visual stimuli (Study 2) evoked by hand movements or saccades. Their findings suggested stronger SA when hand movements produced sounds and saccades elicited visual stimuli, indicating a connection between sensory attenuation and the likelihood of a causal link between motor actions and the modality of their sensory consequences. Examining congruency from the perspective of the stimulated hemifield, [Buaron et al. \(2020\)](#) reported enhanced perceptual modulation for laterally presented abstract stimuli triggered by the congruent (ipsilateral) versus incongruent (contralateral) hand. Similarly, regarding self-generated sounds, [Reznik et al. \(2014\)](#) reported lower monaural hearing thresholds when the sound triggering hand was congruent (ipsilateral) with the stimulated ear. Considering the laterality of the stimulus-triggering hand, [Buaron et al. \(2020\)](#) also reported distinct neural activity in the visual cortex depending on the identity of the moving hand, despite identical visual outcome.

Our findings of stronger SA effects in stimulus/hemifield-congruent compared to incongruent experimental conditions corroborate the conclusions of the aforementioned studies, although they do not allow us to differentiate between the role of stimulus identity (LH vs. RH) and stimulus laterality (left vs. right hemifield).

#### 4.4. Limitations

While our study has substantial strengths, such as the inclusion of non-right-handed participants, and the examination of congruency between movement and stimulus laterality in the context of SA, we acknowledge that it is subject to several limitations that are worth considering in the interpretation of our findings. Firstly, while our participant pool displayed a diverse range of hand dominance, it is noteworthy that our sample predominantly consisted of strongly right-handed participants, potentially skewing our findings. Therefore, moving forward, it would be necessary to recruit a more balanced representation of the left-handed and ambidextrous population to thoroughly validate the interpretations of the current results. Secondly, it is

important to highlight that the contingent paradigm employed in the current study has recognized shortcomings (Horváth, 2015). Specifically, it does not allow proper experimental control for the confounding impact of temporal attention, which could have primarily influenced the P1/N1 components. Both our current and previous findings support the proposition that the P1 is simultaneously subject to attentional amplification and prediction-based suppression. This aligns with the suppression effects reported by Ody et al. (2023) in a paradigm that meticulously controlled for attentional bias. In future studies, it will be crucial to systematically examine the attention vs. prediction interaction view concerning the P1, and more adequately control for confounding factors.

#### 4.5. Conclusion

The present study revealed that sensory attenuation during the initial stages of visual processing (C1 component) appears to be a general phenomenon, evident across varying degrees of handedness, as well as stimulus/movement combinations. Nevertheless, the degree of C1 suppression was modulated by handedness in a manner associated with the preferential processing of stimuli associated with the dominant hand, presented in the dominant hemifield, elicited by actions of the dominant hand, but only for right-handed participants. The modulation of the P1 was indicative of the simultaneously present but opposing influences of attention and prediction. P1 suppression was more pronounced above the hemisphere contralateral to the side of movement, an effect that was substantially stronger in left-handed individuals. We propose that the observed effects of handedness may be rooted in functional/anatomical asymmetries in the processing of body parts (C1) and attention networks (P1). Our findings demonstrate the modulating effect of hand dominance as well as action-outcome congruency on sensory attenuation and emphasize the necessity for further investigation into the specific interplay between these factors. Ultimately, further empirical evidence pointing toward the same direction may support a premotor account for movement-related early sensory neural phenomena in the visual domain.

#### CRedit authorship contribution statement

**Viktória Roxána Balla:** Writing – original draft, Visualization, Validation, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Tünde Kilencz:** Writing – review & editing, Investigation, Conceptualization. **Szilvia Szalóki:** Writing – review & editing, Investigation, Conceptualization. **Vera Daniella Dalos:** Writing – review & editing, Investigation, Conceptualization. **Eino Partanen:** Writing – review & editing, Supervision. **Gábor Csifcsák:** Writing – review & editing, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

#### Declaration of competing interest

The authors declare no conflicts of interest.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ijpsycho.2024.112344>.

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