Title: Action-associated modulation of visual event-related potentials evoked by abstract and ecological stimuli

Running head: Action-associated visual ERP modulations

Gábor Csifcsák[a,b], Viktória Roxána Balla[a], Vera Dalos[a], Tünde Kilencz[a], Edit Magdolna Biró[a], Gábor Urbán[a], Szilvia Szalóki[c]

[a]Department of Cognitive and Neuropsychology, Institute of Psychology, Faculty of Arts, University of Szeged, Egyetem u. 2, 6722 Szeged, Hungary

[b]Department of Psychology, University of Tromsø, Huginbakken 32, 9037 Tromsø, Norway

[c]Department of Psychiatry, Faculty of Medicine, University of Szeged, Kálvária sgt. 57, 6725 Szeged, Hungary

Corresponding author: Gábor Csifcsák, Department of Psychology, UiT The Arctic University of Norway, Huginbakken 32, 9037 Tromsø, Norway, Phone: +47 77 64 67 76, Fax: +47 77 64 52 91, Email: gabor.csifcsak@uit.no

Abstract

This study investigated the influence of action-associated predictive processes on visual event-related potentials (ERPs). In two experiments (N=17 and N=19), we sought evidence for sensory attenuation (SA) indexed by ERP amplitude reductions for self-induced stimuli when compared to passive viewing of the same images. We assessed if SA (1) is stronger for ecologically valid versus abstract stimuli (by comparing ERPs to pictures depicting hands versus checkerboards), (2) is specific to stimulus identity (certain versus uncertain action-effect contingencies), and (3) is sensitive to laterality of hand movements (dominant versus subdominant hand actions). We found reduced occipital responses for self-triggered hand stimuli very early, between 80-90 ms (C1 component), but this effect was absent for checkerboards. On the contrary, the P1 component (100-140 ms) was enhanced for all action-associated stimuli, and this effect proved to be sensitive to stimulus predictability for hands only. The parietal N1 component (170-190 ms) showed amplitude enhancement after right-hand movements for checkerboards only. Overall, our findings indicate that action-associated predictive processes attenuate early cortical responses to ecologically valid visual stimuli. Moreover, we propose that subsequent ERPs show amplitude enhancement that might result from the interaction between expectation-based SA and attention. Movement-initiated modulation of visual ERPs does not appear to show strong lateralization in healthy individuals, although the absence of lateralized effects cannot be excluded. These results can have implications for assessing the influence of action-associated predictions on visual processing in psychiatric disorders characterized by aberrant sensory predictions and alterations in hemispheric asymmetry, such as schizophrenia.

Keywords: visual event-related potentials, sensory attenuation, agency, motor prediction, lateralization

1. Introduction

When reaching out for an object, we typically rely on sensory feedback such as proprioceptive signals that convey information about muscle stiffness and joint movements. At the same time, visual information might be crucial for calculating appropriate movement trajectories. Given the strong association between hand movements and the sight of the corresponding hand, it is likely that this specific visual feedback also contributes to the sense of agency, that is, to feelings about being in control of one's own actions and their sensory consequences (Christoff, Cosmelli, Legrand, & Thompson, 2011; Gallagher, 2000). Sensory attenuation (SA) is among the few phenomena that have been associated with the sense of agency (Haggard & Eitam, 2015). SA refers to increased discrimination thresholds and reduced neural signals to stimuli generated by self-initiated actions (Bäss, Jacobsen, & Schröger, 2008; Blakemore, Frith, & Wolpert, 1999; Blakemore, Wolpert, & Frith, 1998; Roussel, Hughes, & Waszak, 2014; Weiss, Herwig, & Schütz-Bosbach, 2011). According to the comparator model (Blakemore, Wolpert, & Frith, 2002), a central copy of the motor command enables forming precise predictions ('forward internal models') about the forthcoming sensory consequences of that action. If predictions and feedback signals match, stimulus processing becomes attenuated relative to a mismatch because predictions elicit 'corollary discharges' in sensory areas that dampen the processing of reafferent signals (Heinks-Maldonado et al., 2007; Horváth, 2015; Wolpert, Ghahramani, & Jordan, 1995). Alternatively, it has been proposed that SA arises because a mismatch between anticipated and detected stimuli elicits larger prediction error ('surprise') signals that prompt updating existing models about action-effect associations (Schröger, Marzecová, & SanMiguel, 2015). The comparator model has been used to explain symptoms of several neuropsychiatric conditions such as the abnormal sense of agency in anarchic hand syndrome or delusions of control in schizophrenia (Blakemore et al., 2002; Ford, Gray, Faustman, Roach, & Mathalon, 2007; Heinks-Maldonado et al., 2007). However, other accounts have also been put forward as the comparator model proved to be insufficient for explaining all phenomena related to the sense of agency and its pathology (Frith, 2012).

The majority of studies set to investigate the neural underpinnings of action-associated sensory processing in humans focused on the somatosensory and auditory systems, and found converging neuroimaging and electrophysiological evidence for SA (Bäss et al., 2008; Blakemore et al., 1998; Christoffels, Formisano, & Schiller, 2007; Martikainen, Kaneko, & Hari, 2004). With respect to auditory event-related potentials (ERPs) recorded by electroencephalography (EEG), reduced amplitude of the N1 component for self-initiated sounds is probably the most consistent finding in this field (for review see: Schröger, Marzecová, & SanMiguel, 2015). While these results are consistent with the comparator model, several authors raised concerns about this interpretation and highlighted potential confounds such as the influence of temporal attention or unspecific sensory gating during action execution (Horváth, 2015; Horváth, Maess, Baess, & Tóth, 2012; Hughes, Desantis, & Waszak, 2013b; Lange, 2013). Along these lines, studies reporting enhanced (rather than reduced) hemodynamic responses in the somatosensory cortex during self-initiated stimulation (Ackerley et al., 2012) or the absence of auditory N1 suppression during vocalization (Chen, Chen, Liu, Huang, & Liu, 2012) have argued for the confounding effect of attention.

Results are even more perplexing in the visual domain, since both increased and reduced visual ERPs have been found for action-associated vs. externally controlled stimuli (Benazet, Thénault, Whittingstall, & Bernier, 2016; Gentsch, Kathmann, & Schütz-Bosbach, 2012; Gentsch & Schütz-Bosbach, 2011; Gentsch, Schütz-Bosbach, Endrass, & Kathmann, 2012; Hughes & Waszak, 2011; Mifsud et al., 2016; Schafer & Marcus, 1973). Moreover, there is no consensus on the scalp topography (anterior vs. posterior) and timing (around 100 ms vs. around 150 ms vs. between 200-350 ms) of such effects. Importantly, the earliest ERP components to show SA for self-initiated visual stimuli are the anterior N1 (peaking between 80-130 ms post-stimulus) and the posterior N1 (peaking between 140-200 ms) (Gentsch, Kathmann, et al., 2012; Gentsch & Schütz-Bosbach, 2011; Gentsch, Schütz-Bosbach, et al., 2012; Schafer & Marcus, 1973), but these results could not be replicated by other authors (Hughes & Waszak, 2011; Mifsud et al., 2016). The absence of clear SA for early visual ERPs is rather strange given

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the fact that SA was first proposed for the suppression of visual processing during saccades by Helmholtz (Von Helmholtz, 1867), and neural signatures of this phenomenon can be detected very early, even during subcortical processing (Reppas, Usrey, & Reid, 2002; Thilo, Santoro, Walsh, & Blakemore, 2004).

The degree of correspondence between predicted and experienced sensory inputs was shown to influence the sense of agency (Sato & Yasuda, 2005). In line with this, behavioral and EEG correlates of SA are more prominent for action-congruent sensory feedbacks (Bäss et al., 2008; Heinks-Maldonado et al., 2007; Hughes, Desantis, & Waszak, 2013a; Roussel et al., 2014; Weiss et al., 2011). For auditory ERPs, Bäss et al. (2008) found attenuated N1 component for action-associated stimuli even when presented with an unpredictable frequency and/or onset, but the degree of amplitude reduction was larger for completely predictable tones. This result underlines the importance of precise motor-based sensory predictions that can be sensitive to stimulus identity as well as timing (see also: Hughes et al., 2013). So far, three visual ERP studies assessed the effect of stimulus predictability on the processing of self-initiated stimuli, but neither included a non-motor condition with passive viewing, nor did they present completely predictable stimuli (action-effect contingencies varied between 47.5-75%) (Hughes, 2015; Hughes & Waszak, 2014; Roussel et al., 2014). Still, all studies reported attenuated posterior ERP amplitudes for more predictable stimuli (albeit in different time intervals), which effect is reminiscent to those obtained in the auditory modality (Bäss et al., 2008; Hughes et al., 2013a).

Given that the processing of relatively simple and abstract stimuli such as sinusoidal tones or checkerboards does not necessarily translate to real-world situations, it is important to test if similar effects apply to complex images and ecologically more valid scenarios. With respect to SA, this issue has been thoroughly investigated in the auditory domain, by analyzing ERPs evoked by vocalized sounds (Ford et al., 2007; Heinks-Maldonado et al., 2007). Similar approaches in the visual domain are surprisingly scarce. We are aware of only one study that evaluated cortical responses to visual feedback about trajectories of reaching arm movements (Benazet et al., 2016). Feedbacks constituted of moving dots, either presented in real-time or with 150 ms delay. The main finding was the reduction of the parietal

N1 peak in the real-time condition, which was interpreted as the neural signature of smaller prediction errors for movement-congruent visual reafferent signals. However, no study in this field used pictures depicting hands as feedbacks following hand movements, despite these stimuli being perhaps the most salient changes in the visual environment during voluntary actions in everyday life.

Action-associated neural processes show signs of hemispheric lateralization in the auditory modality. Oscillatory responses during overt vocalization were observed above the left hemisphere only, which is not surprising given the lateralization of linguistic function (Ford, Mathalon, Whitfield, Faustman, & Roth, 2002). Moreover, hemodynamic responses in the auditory cortex were found to be influenced to a stronger degree when music sequences were produced by the contralateral hand, indicated that lateralization is also present for non-verbal stimuli (Reznik, Henkin, Schadel, & Mukamel, 2014). Given the strong association between hand actions and the sight of the moving hand, these findings raise the question if visual SA would also be sensitive to hand identity (i.e., to movements either being controlled by the dominant or the subdominant hemisphere), especially for pictures of the corresponding hand as feedback stimuli. Interestingly, the visual system was shown to automatically monitor hand identity, being more sensitive to unexpected hand laterality for the dominant (right) hand, with neural responses localized in the dominant (left) hemisphere (Stefanics & Czigler, 2012). Despite this, lateralization of movement-associated SA in the visual modality has not been investigated to our knowledge.

The current study consisted of two experiments that tested four hypotheses. First, by focusing on three posterior components (the C1, P1 and N1), we expected to find ERP evidence for SA for self-initiated stimuli. Given the controversy in the literature (Benazet et al., 2016; Gentsch, Schütz-Bosbach, et al., 2012; Hughes & Waszak, 2011; Mifsud et al., 2016; Schafer & Marcus, 1973), we did not formulate precise predictions on the timing of SA, nor did we exclude the possibility of measuring amplified responses to any of these components. Second, by comparing experimental blocks with certain and uncertain stimulus predictability, we anticipated stronger SA for certain action-effect contingency, which

result would be in accordance with findings in the auditory domain (Bäss et al., 2008) and also with the comparator model of action-associated predictions about effect identity. Third, we compared the magnitude of SA for abstract (checkerboard) and ecological (hand) stimuli and expected to find stronger SA for the latter. Finally, we asked participants to perform movements with their both hands (in separate blocks) and tested if SA would show any sign of lateralization. Here, we hypothesized stronger SA for actions performed by the dominant hand primarily for pictures depicting hands, and we also anticipated that SA would be more prominent above the hemisphere contralateral to hand movement, because that hemisphere produces the motor command and therefore, it might be more involved in the generation of predictions. The overall design of the two experiments was very similar, with Experiment 1 focusing on the processing of checkerboards and Experiment 2 assessing the cortical analysis of hand stimuli.

2. Experiment 1

2.1 Methods

2.1.1 Participants

Eighteen healthy adults, were recruited in Experiment 1. Data of one participant was excluded due to temporary technical problems with the EEG system, and therefore, the final analysis was conducted with data from 17 subjects (9 female; age range: 19-35 years; M_{age} = 24.0 years, SD = 3.8). All participants had normal or corrected-to-normal vision, none suffered from current or past psychiatric or neurological conditions (based on self-report). We used the Edinburgh Handedness Inventory (Oldfield, 1971) to assess handedness, all participants were right-handed (score range: 42-100; M = 72.17, SD = 21.00). 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.

2.1.2 Stimuli and procedure

Data collection was performed in a dark, sound-proof room. Participants sat in a comfortable chair, 80 cm in front of a 20-inch LCD screen (LG Flatron; resolution: 1024 × 768; refresh rate: 75 Hz; rectangular temporal window). Checkerboards consisting of 1.65° black and white checks (full stimulus size: 10 x 13.2°; luminance: 15.2 cd/m^2) were presented for 300 ms on a black background, using E-Prime (Psychology Software Tools, Sharpsburg, PA, USA). In certain stimulus predictability (CSP) blocks, checkerboards were always oriented vertically, while in blocks with uncertain stimulus predictability (USP), vertically and horizontally oriented checkerboards were presented in a random order, with equal probability (Figure 1). A red "+" sign (size: 0.6°) was used as fixation stimulus and was always present on the center of the screen.
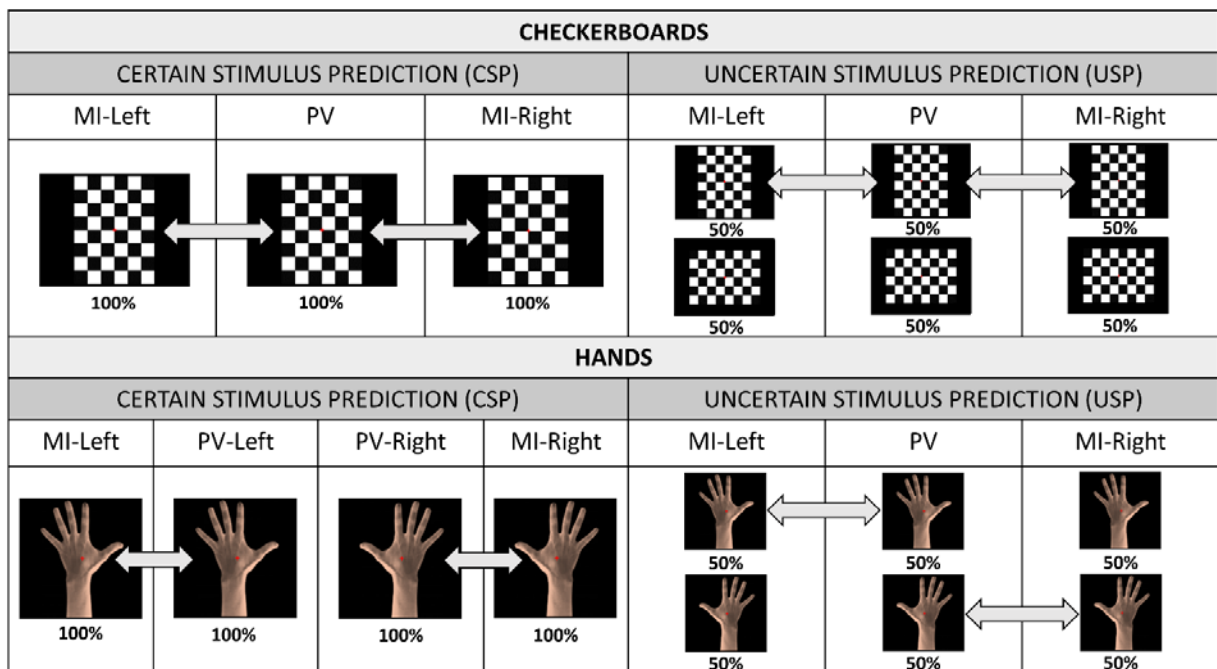

Figure 1. Overview of the experimental conditions that were used to contrast neural responses for passively viewed versus self-initiated stimuli (please note that the motor-only condition that was used for correcting event-related potentials for motor activity is not shown). MI: motor-induced condition; PV: passive viewing condition.

We adapted the contingent paradigm, which typically consists of three experimental conditions: passive viewing (PV), motor-induced (MI) and motor-only (MO). During PV, stimuli appeared with a

randomized interstimulus interval of 1700-3500 ms while participants were asked to maintain fixation. In MI blocks, participants were required to press the spacebar with either their left or right hand in a self-paced manner, aiming at a rhythm of about 2-3 seconds. They were asked to keep their fingers (except for the thumb) positioned on the spacebar and to avoid moving their wrists or elbows. Participants were instructed that the software would not respond to very fast responses (1500 ms, unbeknownst to the participants) and that they should also avoid very slow responding. In addition, they were asked to avoid counting the time elapsed between two key presses, as the exact timing of responding would not be crucial in the experiment. Participants had to maintain fixation and were told that each motor response would be immediately followed by a briefly presented stimulus. In MO blocks, subjects were asked to produce self-paced finger movements identical to those in the MI task, while fixating at the fixation stimulus. No checkerboards were presented in these blocks.

The whole experiment consisted of 11 blocks (100 trials in each): 2 MO blocks (MO-Left and MO-Right for left- and right-hand responses, respectively), 6 MI blocks (3-3 MI-Left and MI-Right; one CSP and two USP blocks for each hand), and 3 PV blocks (one CSP and two USP blocks). The order of PV, MI-Left, MI-Right, MO-Left and MO-Right blocks was counterbalanced across participants, but for the PV, MI-Left and MI-Right conditions, we always started with the CSP block, followed by two USP blocks. Given that only 50 vertical checkerboards were presented in USP blocks, we included two blocks to obtain a total of 100 stimuli for vertical checkerboards, enabling comparison with CSP blocks of the same trial number. The mean duration of PV blocks was 4.83 minutes, whereas MI and MO blocks lasted for around 5-7 minutes, depending on individual response times. Participants could have a short rest between the blocks. Each MO and MI block started with a short practice consisting of 10 trials, during which immediate feedbacks about response times were provided in order to get acquainted with the task requirements.

2.1.3 EEG recording and analysis

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EEG was recorded with a Biosemi ActiveTwo Amplifier (BioSemi, Amsterdam, The Netherlands) at a sampling rate of 1024 Hz, using 32 scalp Ag/AgCl electrodes placed in accordance with 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, and O2). In addition, two electrodes were placed at the outer canthi of both eyes to record horizontal electrooculogram (EOG), and another two were placed above and below the midline of the left eye to record vertical EOG. The recording reference and the ground electrodes (Common Mode Sense and Driven Right Leg electrodes in the ActiveTwo system) (Metting, Peper, & Grimbergen, 1990) were placed in close proximity to the Cz position. Data was collected without applying frequency filters.

EEG was analyzed with the EEGLAB (Delorme & Makeig, 2004) and ERPLAB (Lopez-Calderon & Luck, 2014) toolboxes for Matlab (MathWorks, Natick, MA, USA). Continuous EEG was re-referenced to the Fz electrode and band-pass filtered between 0.5-30 Hz using an infinite impulse response Butterworth filter (12dB/oct). Ocular artifacts and other generic discontinuities were removed with independent component analysis (ICA) implemented in the ADJUST plugin for EEGLAB (Mognon, Jovicich, Bruzzone, & Buiatti, 2011). This method yielded at least 80 artifact-free epochs for all participants and stimulus conditions. Data was epoched between 100 ms pre- and 600 ms poststimulus, baseline corrected (-100 ms to 0 ms) and averaged for each condition separately. In USP blocks, only trials with vertical checkerboards were analyzed. To remove neural activity associated with motor preparation and execution in MI blocks, ERPs obtained in MO blocks were subtracted from MI data of the corresponding hand (corrected motor-induced condition; C-MI). This way, PV and C-MI data could be compared directly to assess changes in visual processing related to action-associated predictive processes. Mean baseline-to-peak C1, P1 and N1 amplitudes were extracted at posterior channels (C1: Oz; P1: O1/Oz/O2; N1; P7/P8) in the 80-90 ms, 100-140 ms and 170-190 ms time windows, respectively. These time intervals and channels were determined by visual inspection of group-averaged data (Supplementary

Figure 1), and they are also in line with data extraction procedures of previous studies (Gentsch, Schütz-Bosbach, et al., 2012; Hughes & Waszak, 2011, 2014).
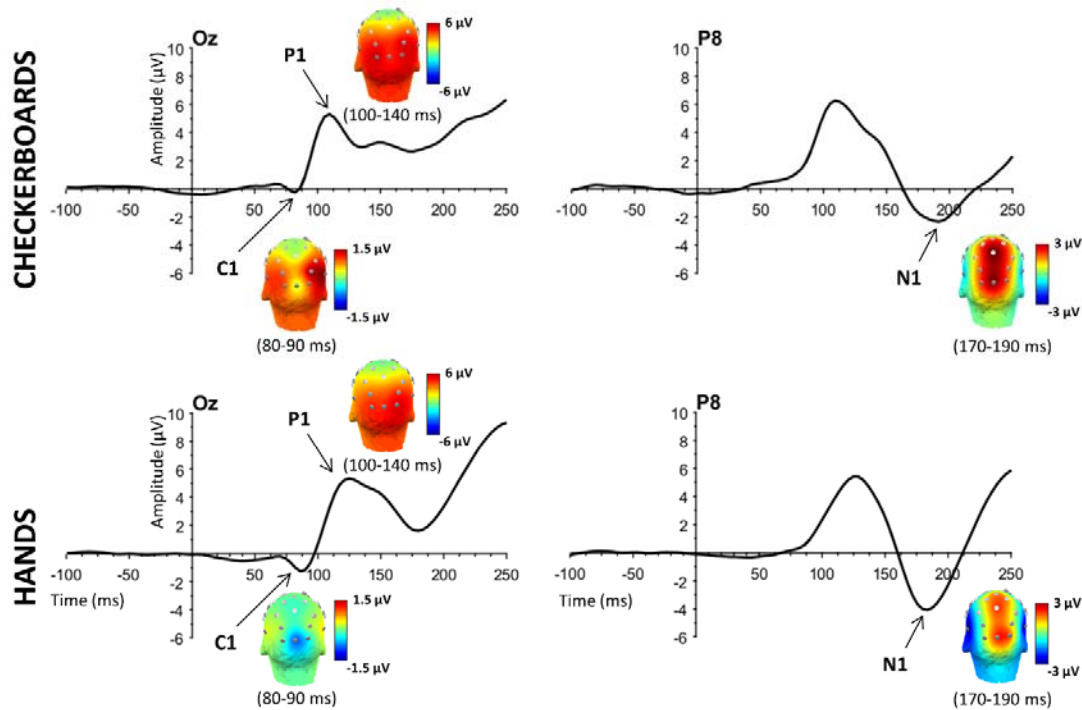
Supplementary Figure 1. Grand-averaged event-related potentials obtained in the passive viewing conditions (collapsed for certain and uncertain stimulus predictability) of Experiment 1 (checkerboards) and Experiment 2 (hands), shown at electrodes Oz and P8.

2.1.4 Statistical analysis

For all three ERP components, separate ANOVAs were performed for the PV vs. C-MI-Left and PV vs. C-MI-Right comparisons, with CONDITION (2 levels: PV, C-MI-Left or C-MI-Right), PREDICTABILITY (2 levels: CSP, USP) and ELECTRODE (P1: 3 levels, N1: 2 levels) as within-subject factors. Alpha level was set to .05; significant interactions were further evaluated with Bonferroni-corrected post hoc tests. For violations of sphericity (verified by Mauchly's test), Greenhouse-Geisser corrected *p* values and the relevant epsilon (ε) correction are reported. Partial eta-squared (η_p^2) values are also show to demonstrate effect size.

2.2 Results

Group averaged ERPs for PV and for left- or right-hand associated C-MI blocks are shown in Figure 2, separately for CSP and USP stimulus arrangements. The posterior scalp distribution of difference waves (PV – C-MI) calculated for time windows corresponding to the C1, P1 and N1 components are shown in Figure 3, separately for each hand movement and for CSP or USP blocks. The effect of correction for movement-related neural activity to obtain C-MI ERPs (i.e., the calculation of the MI – MO difference waveform) is shown in Supplementary Figure 2.
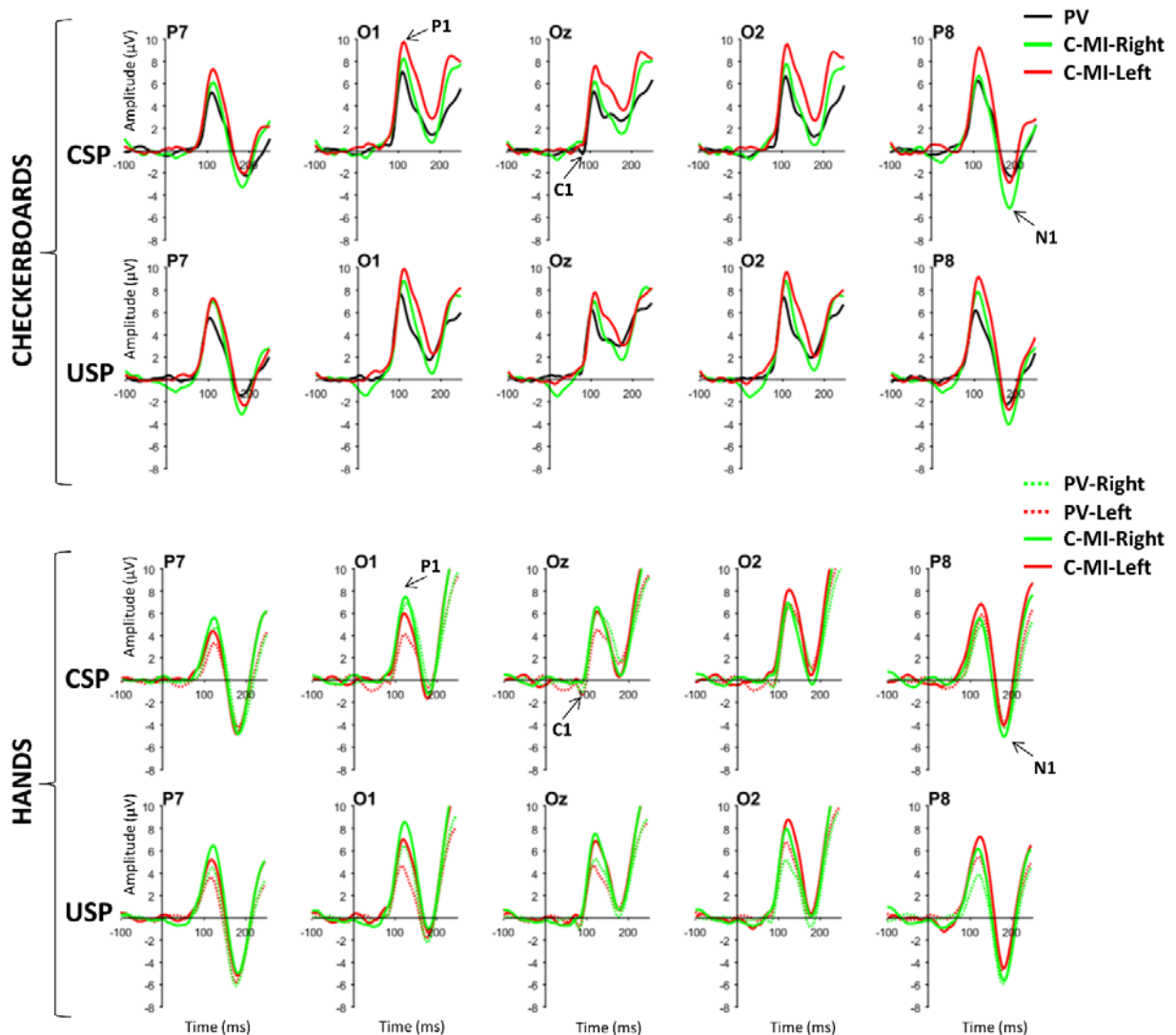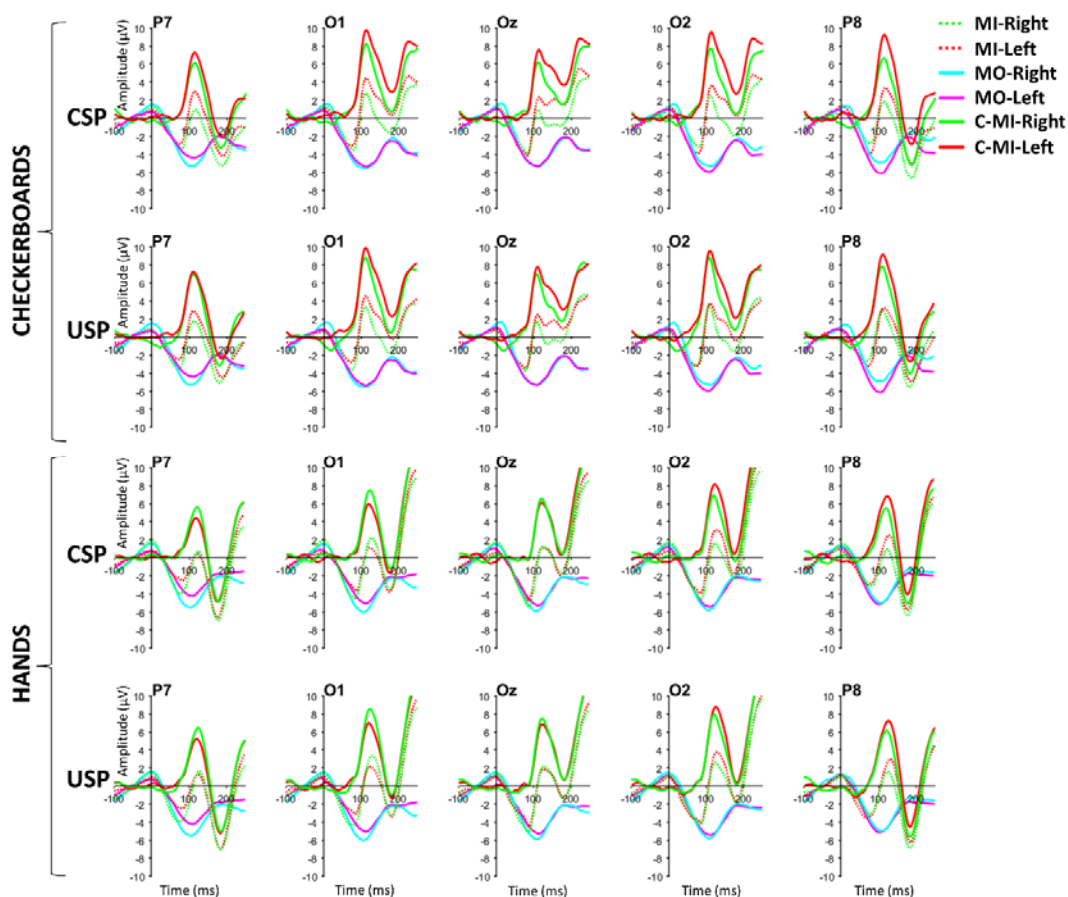

Figure 2. Event-related potentials obtained in Experiment 1 (checkerboards) and Experiment 2 (hands) at five posterior electrodes. C-MI: corrected motor-induced condition; CSP: certain stimulus predictability; PV: passive viewing condition; USP: uncertain stimulus predictability.

2.2.1 The C1 component

For the C1 component, repeated-measures ANOVA revealed a main effect of PREDICTABILITY both for the PV vs. C-MI-Left ($F(1,16) = 15.34$, $p = .001$, $\eta_p^2 = .49$) and the PV vs. C-MI-Right comparisons ($F(1,16) = 5.77$, $p = .029$, $\eta_p^2 = .26$), as C1 amplitudes were larger in CSP relative to USP blocks (Figure 2). Moreover, the interaction between CONDITION and PREDICTABILITY was significant for the PV vs. C-MI-Right comparison ($F(1,16) = 5.51$, $p = .032$, $\eta_p^2 = .26$), because the C1 was enhanced in CSP blocks during passive viewing only ($p = .001$). With respect to the amplitude difference between PV and C-MI-Right blocks, only a tendency was found for a reduced C1 after right-hand actions in CSP blocks ($p = .075$).

Supplementary Figure 2. Raw waveforms obtained for all experimental conditions in Experiment 1 (checkerboards) and Experiment 2 (hands) at the five posterior electrodes. C-MI: corrected motor-induced condition; CSP: certain stimulus predictability; MI: motor-induced condition; MO: motor-only condition; USP: uncertain stimulus predictability.

2.2.2 The P1 component

Regarding the P1 amplitude, the main effect of ELECTRODE was significant for the PV vs. C-MI-Left ($F(2,32) = 5.39$, $\varepsilon = .66$, $p = .01$, $\eta_p^2 = .25$) and PV vs. C-MI-Right comparisons ($F(2,32) = 5.14$, $p = .012$, $\eta_p^2 = .24$), since this component was reduced at Oz relative to O1 ($p < .03$ for both comparisons) and a similar trend was present when compared to O2 (PV vs. C-MI-Left: $p = .069$; PV vs. C-MI-Right: $p = .054$). Crucially, we found larger P1 amplitudes in both C-MI conditions than in PV (PV vs. C-MI-Left: $F(1,16) = 14.67$, $p = .001$, $\eta_p^2 = .48$; PV vs. C-MI-Right: $F(1,16) = 8.19$, $p = .011$, $\eta_p^2 = .34$; Figures 2-3). This was qualified by an interaction between CONDITION and ELECTRODE for the PV vs. C-MI-Left comparison ($F(2,32) = 3.83$, $p = .032$, $\eta_p^2 = .19$), because here, the P1 was smaller at Oz relative to O1 and O2 after hand movements ($p < .04$) but not during passive viewing ($p > .09$). However, P1 amplitudes after left-hand actions were enhanced at all three electrodes ($p < .007$ for all comparisons). Other effects were not significant.

2.2.3 The N1 component

In the case of the posterior N1, no significant main effects or interactions were found for the PV vs. C-MI-Left comparison. As for the ANOVA with the PV vs. C-MI-Right contrast, the main effect of CONDITION was significant ($F(1,16) = 4.96$, $p = .041$, $\eta_p^2 = .24$), characterized by N1 enhancement after right-hand actions (Figure 2). In addition, we found a significant interaction between CONDITION, PREDICTABILITY and ELECTRODE ($F(1,16) = 6.61$, $p = .020$, $\eta_p^2 = .29$), due to significantly smaller N1 amplitudes for PV relative to C-MI-Right in CSP blocks above the right hemisphere (P7: $p = .191$; P8: $p = .046$) and a similar trend in USP blocks above the left hemisphere (P7: $p = .024$; P8: $p = .051$). Other post hoc tests were not significant.
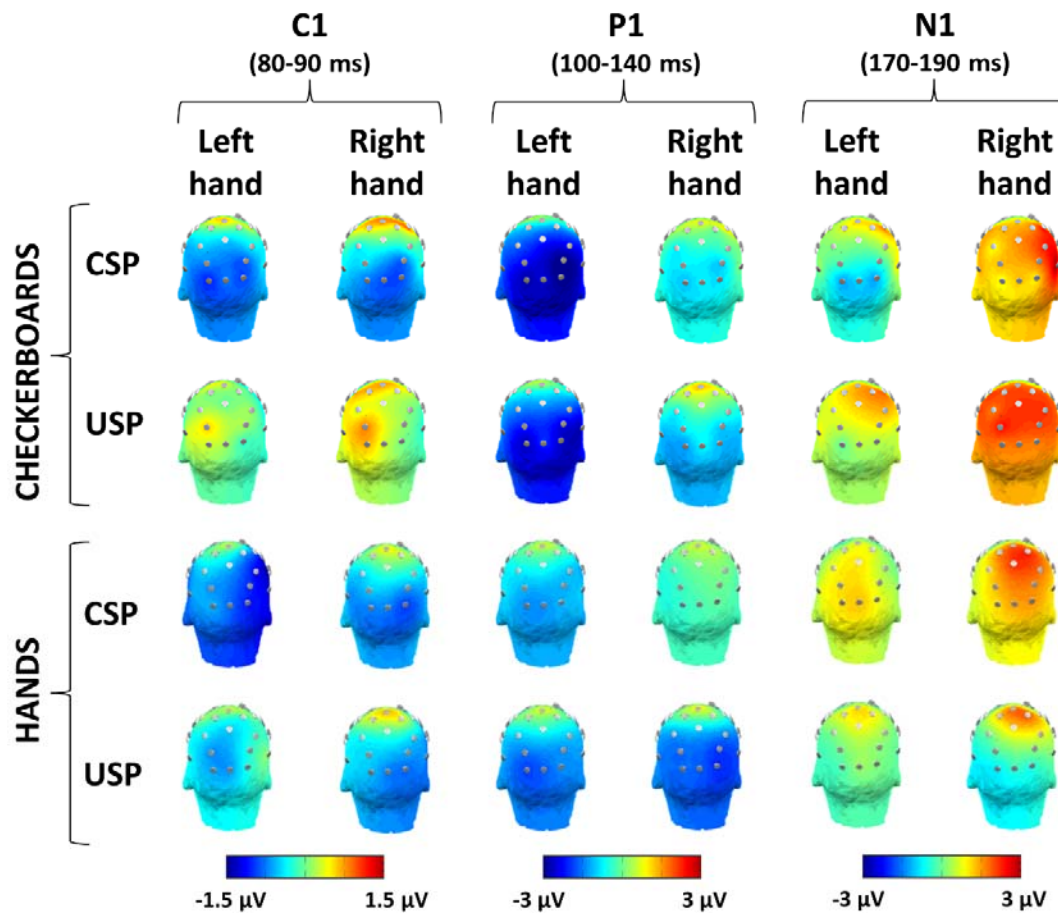
Figure 3. Posterior scalp topography of difference waveforms (passive viewing vs. corrected motor-induced), obtained in Experiment 1 (checkerboards) and Experiment 2 (hands). For each event-related potential, mean activity was calculated within the respective time windows. CSP: certain stimulus predictability; USP: uncertain stimulus predictability.

3. Experiment 2

3.1 Methods

3.1.1 Participants

Twenty-two healthy adults participated in Experiment 2. Three participant were excluded due to extensive artifacts and/or low signal-to-noise ratio. Thus, data from 19 subjects (10 female; age range: 19-38 years; M_{age} = 25.7 years, SD = 6.0) was analyzed. All participants were right-handed (Edinburgh Handedness Inventory score range: 42-100; M = 76.15, SD = 18.05), had normal or corrected-to-normal

vision, none suffered from current or past psychiatric or neurological conditions (based on self-report). 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.

3.1.2 Stimuli and procedure

The procedure was very similar to the one used in Experiment 1, with few important exceptions. The right-hand stimulus was a computer-designed image depicting the dorsum of the right hand and the distal 1/3 of the forearm (size: 10 x 12.6°; luminance: 4.3 cd/m^2), while its mirror image was used in left-hand blocks (Figure 1). In this experiment, a total of 12 blocks were used: 2 MO (identical to those in Experiment 1), 6 MI (3-3 MI-Left and MI-Right; for each movement type we started with one CSP block during which only hand stimuli congruent with the hand performing the action were presented, followed by two USP blocks with 50-50 % left- and right-hand stimuli appearing in a random order) and 4 PV blocks (2 CSP with either exclusively left- or right-hand stimuli and 2 USP with left- and right-hand stimuli presented randomly, with equal probability). The order of PV, MI-Left, MI-Right, MO-Left and MO-Right blocks was counterbalanced across participants. Blocks were separated by short breaks. Each MO and MI block started with a practice consisting of 10 trials with immediate feedbacks about response times.

3.1.3 EEG recording and analysis

Data recording and analysis was identical to that reported in Experiment 1, with the exception that here, data for both stimulus types in PV-USP blocks were used in the analysis, because they were compared to data obtained for the same stimulus in C-MI-USP blocks. In other words, EEG responses to left-hand stimuli in PV-USP blocks were compared to those for left-hand stimuli in MI-Left-USP blocks (after performing motor correction by subtracting MO-Left ERPs) and conversely, right-hand stimuli from

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PV-USP blocks were compared to right-hand stimuli from MI-Right-USP blocks (after correction with MO-Right data).

3.1.4 Statistical analysis

Given that in this experiment we included two PV-CSP blocks with either exclusively left- or right-hand stimuli, repeated-measures ANOVAs for ERPs contained CONDITION (2 levels: PV and C-MI), HAND (2 levels: left- and right-hand stimuli), PREDICTABILITY (2 levels: CSP, USP) and ELECTRODE (P1: 3 levels, N2: 2 levels) as within-subject factors. All other details for ERP analysis are identical to those reported in Experiment 1.

3.2 Results

3.2.1 The C1 component

The C1 was significantly reduced in amplitude after hand movements relative to passive viewing (main effect of CONDITION: $F(1,18) = 4.80$, $p = .042$, $\eta_p^2 = .21$; Figure 2). No other main effects or interactions were significant.

3.2.2 The P1 component

Similarly to the results of Experiment 1, the P1 was enhanced for C-MI stimuli (main effect of CONDITION: $F(1,18) = 13.93$, $p = .002$, $\eta_p^2 = .44$; Figures 2-3). The interaction between CONDITION and PREDICTABILITY was nearly significant ($F(1,18) = 4.42$, $p = .050$, $\eta_p^2 = .2$), with post hoc comparisons showing increased P1 in USP relative to CSP blocks after hand movements only (CSP vs. USP difference for PV: $p = .532$; for C-MI: $p = .018$). The difference between PV vs. C-MI amplitudes was significant for both the CSP and USP blocks ($p < .011$). The main effect of ELECTRODE was also significant ($F(2,36) = 5.18$, $p = .011$, $\eta_p^2 = .22$), since this component was smaller at Oz than at O2 ($p = .003$). Despite the significant PREDICTABILITY x ELECTRODE interaction ($F(2,36) = 9.92$, $\varepsilon = .67$, $p = .002$, $\eta_p^2 = .35$), both the CSP and USP blocks were characterized by a similar electrode effect ($p < .01$

for all comparisons), while the a trend for larger P1 in USP relative to CSP blocks was also found above the left hemisphere (at O1: $p = .51$). In addition, we found a significant interaction between HAND and ELECTRODE ($F(2,36) = 29.47$, $\varepsilon = .65$, $p < .001$, $\eta_p^2 = .62$), which was due to a larger P1 amplitude for right-hand relative to left-hand stimuli at O1 ($p = .002$), a similar trend at Oz ($p = .065$) and enhanced P1 for left-hand relative to right-hand images at O2 ($p = .025$). This effect was primarily driven by a larger P1 for left-hand stimuli at O2 (O2 vs. Oz: $p < .001$; O2 vs. O1: $p < .001$), whereas the P1 evoked by right-hand stimuli was comparable at all three electrode sites ($p > .09$ for all comparisons; Supplementary Figure 3). Other main effects or interactions were not significant.[1]
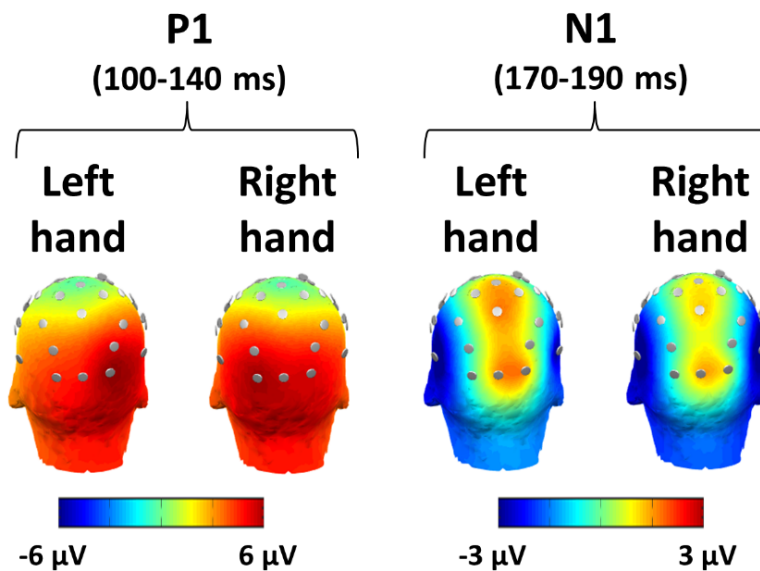
Supplementary Figure 3. Posterior scalp topography of waveforms (mean activity calculated within the respective time windows) obtained for all left- and right-hand stimuli in Experiment 2.

3.2.3 The N1 component

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[1] We note the nearly significant CONDITION x HAND x PREDICTABILITY x ELECTRODE interaction ($F(2,36) = 3.66$, $\varepsilon = .67$, $p = .056$, $\eta_p^2 = .17$), with significant PV vs. C-MI post hoc differences for left-hand CSP, left-hand USP and right-hand USP stimuli at all three electrode sites ($p < .023$ for all comparisons), but no amplitude modulations after right-hand movements (relative to passive viewing) in CSP blocks ($p > .23$ for all electrodes). This is consistent with the posterior scalp distributions shown in Figure 3, with a substantially smaller negative difference (PV – C-MI) for right-hand CSP stimuli.

The N1 component was significantly larger in USP blocks (main effect of PREDICTABILITY: $F(1,18) = 14.82$, $p < .001$, $\eta_p^2 = .45$), an effect that was qualified by an interaction between CONDITION and PREDICTABILITY ($F(1,18) = 6.24$, $p = .022$, $\eta_p^2 = .26$) and by a significant triple interaction between CONDITION, PREDICTABILITY and ELECTRODE ($F(1,18) = 5.35$, $p = .033$, $\eta_p^2 = .23$). Bonferroni-corrected post hoc comparisons revealed that the N1 was larger in USP relative to CSP blocks above both hemispheres during passive viewing (CSP vs. USP for PV at P7: $p < .001$; at P8: $p = .001$), but not after hand movements ($p > .015$). Importantly, the PV vs. C-MI comparison of N1 amplitudes was not significant for any comparison ($p > .57$; Figure 2). Finally, we found a significant HAND x ELECTRODE interaction ($F(1,18) = 9.15$, $p = .007$, $\eta_p^2 = .34$), which was due to enhanced N1 for right-hand relative to left-hand stimuli at electrode P8 ($p = .009$), but not at position P7 ($p = .599$). However, unlike the P1 evoked by hand stimuli, we found no hemispheric lateralization for the N1 amplitude (P7 vs. P8 contrasts for both hands: $p > .24$; Supplementary Figure 3).

4. Discussion

Both theoretical and experimental work pointed out sensorimotor integration within the action-perception cycle to be crucial for experiencing the sense of agency (Blakemore et al., 2002; Christoff et al., 2011; Gallagher, 2000). Motor-based predictive processes seem to manifest in attenuated early cortical responses to self-induced somatosensory and auditory events (Bäss et al., 2008; Blakemore et al., 1998; Martikainen et al., 2004), however, studies focusing on vision reported both enhanced and suppressed ERPs. By analyzing three posterior visual components, we have also found evidence for both phenomena, albeit in distinct time intervals and with different sensitivities to stimulus type (checkerboards vs. hands), stimulus predictability (certain vs. uncertain) and identity of that hand preforming the action (dominant vs. subdominant). Below, we shall discuss our findings with respect to the contribution of these factors to action-associated ERP modulations.

4.1 Early visual responses are attenuated by action, but only for ecological stimuli

This study was primarily designed to evaluate if action-associated prediction processes shape visual analysis to a similar degree for abstract and ecologically plausible stimuli. We found SA for the posterior C1 component, but only in Experiment 2, where pictures depicting a movement-congruent human hand were presented. This result is important because (1) it shows that SA for early ERPs in present in the visual modality, and (2) that it is already sensitive to the ecological validity of the stimuli. To our knowledge, such early effects of action-associated predictive processes on occipital ERPs have not been reported yet. Gentsch and colleagues found SA for the anterior N1, but this component peaked later, in the P1 interval (Gentsch, Kathmann, et al., 2012; Gentsch & Schütz-Bosbach, 2011). The C1 is generated in the primary visual cortex (Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2002) and probably represents the earliest cortical stage of visual analysis. In this regard, very similar results were reported in the auditory domain, with reduced mid-latency ERPs (the Pa and Nb, both peaking between 20-50 ms) after action initiation (Baess, Widmann, Roye, Schröger, & Jacobsen, 2009). Interestingly, saccadic suppression studies have also shown very early modulations of visual processes (Reppas et al., 2002; Thilo et al., 2004), with movement-associated predictions starting prior to saccade initiation, during the phase of action planning (Bremmer, Kubischik, Hoffmann, & Krekelberg, 2009). Moreover, two studies reported ERP effects prior to hand movements that were suggested to reflect pre-activation of anticipated stimulus representations (Hughes & Waszak, 2011, 2014). Although concerns about the confounding effect of (predominantly temporal) attention have been raised for auditory studies of similar nature (Horváth, 2015; Lange, 2013; Schröger et al., 2015), this is not very likely since the C1 was found to be insensitive to attentional mechanisms (Fu, Fedota, Greenwood, & Parasuraman, 2010; Hillyard & Anllo-Vento, 1998). Thus, we argue that modulations of the C1 component are due to motor-based predictions and their consequential attenuation of visual responses. The fact that we did not observe similar SA for checkerboard stimuli indicates that these early mechanisms are already stimulus-sensitive. This is in line with a study reporting that magnetoencephalographic responses between 50-100 ms are influenced by context-stimulus associations (Chaumon, Drouet, & Tallon-Baudry, 2007). If we consider the course of movement planning and execution as a context that primes the appearance of forthcoming

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stimuli, it is possible that only hand stimuli with stronger response-effect associations could elicit similar context-depend ERP modulations in our study.

4.2 Action-associated P1 and N1 enhancements might reflect interactions between prediction and attention

The P1 component was enhanced in the C-MI (relative to PV) condition in both experiments, indicating that unlike for the C1, this ERP effect is present for both stimulus types. Our result is in accordance with the study by Hughes and Waszak (2011), reporting larger P1 to self-triggered checkerboards. Enhanced ERPs might index more efficient processing of movement-associated stimuli, which can be advantageous for improving task performance, as it has been shown for proprioceptive feedback signals (Gritsenko, Krouchev, & Kalaska, 2007) and has also been suggested for auditory (Reznik et al., 2014) and visual responses (Lebar, Bernier, Guillaume, Mouchnino, & Blouin, 2015). Crucially, Lebar and colleagues (2015) also found larger posterior ERPs to task-irrelevant flashes in high-performer participants during a demanding visually-guided drawing task relative to resting. This result was interpreted as a neural index of a sensory gain control mechanism that increases the weight of visual inputs in a task-dependent manner. In a very similar vein, Hughes and Waszak (2011) proposed attentional orientation towards self-generated stimuli as a potential cause for enhanced P1 amplitudes, since this component was shown to be increased for temporally anticipated visual events (Correa, Lupiáñez, Madrid, & Tudela, 2006; Doherty, Rao, Mesulam, & Nobre, 2005). Finally, the role of attentional processes was emphasized by Mifsud and colleagues (2016), observing larger amplitudes for the occipital N145 (rather than for the P1) in their 'self-initiated' condition. However, to control for temporal predictability, these authors also included an experimental condition in which stimulus onset was externally-cued to aid the build-up of anticipation. Interestingly, neither the P1 nor the N145 were modulated in the cued condition, suggesting that temporal expectation *per se* is not enough for ERP enhancements, and pointing at non-temporal aspects of attention as possible candidates for this effect.

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Attention and expectation have been described to exert opposing (and at times seemingly additive) effects on cortical processing in the auditory and visual domains, with the former increasing and the latter dampening neural responses (Lange, 2013; Schröger et al., 2015; Summerfield & Egner, 2009). As detailed above, it is very likely that both processes were involved in shaping the P1 component in our experiment. We found smaller P1 enhancements for completely predictable (relative to unpredictable) hand feedbacks, especially for those elicited by right-hand actions (Figure 3). This is in contrast with our hypothesis, since we anticipated most robust amplitude modulations for this condition, given the strong reinforcement between dominant-hand actions and the accompanying sight of the corresponding hand. Assuming that attentional effects were relatively similar across conditions (because of low task demands), while the magnitude of SA varied as a function of hand and stimulus identity (Bäss et al., 2008; Reznik et al., 2014), we speculate that the largely similar P1 amplitudes for right-hand movement-induced versus passively viewed completely predictable stimuli reflect greater contribution of predictive processes to SA, counterbalancing the effect of attentional enhancements (see also: Lange, 2013). Although this idea awaits systematic testing in the future, it posits that the P1 component in the contingent paradigm might be both sensitive to movement laterality and to the degree of stimulus predictability, but such effects can be masked by attentional processes.

Finally, action-associated enhancement of the posterior N1 component for checkerboards elicited by the dominant hand is in line with the finding of Mifsud and colleagues (2016). However, it remains puzzling why the N1 effect in Experiment 1 was observed for right-hand actions only, and why (unexpectedly) it showed hemispheric lateralization as a function of stimulus predictability. Nevertheless, we propose that similarly to the P1, the N1 amplitude is also influenced by the interplay between attentional and predictive processes (Correa et al., 2006; Doherty et al., 2005). The absence of movement-based N1 modulation in Experiment 2 can be due to stronger SA for ecologically valid stimuli, dampening the magnitude of attention-related amplitude enhancements. In addition to stimulus type (abstract or ecological), task-relevance of visual feedback signals might also impact the degree of prediction-based SA

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in the N1 time-range. In particular, Benazet and colleagues (2016) reported reduced N1 component for behaviorally relevant moving dots, but only if these provided accurate feedback about movement trajectories in a target reaching task. This effect was restricted to the N1, since neither the preceding P1 nor the subsequent P2 components showed similar modulations. Thus, it is possible that action-associated SA for the N1 is modulated both by stimulus identity and task relevance, being weakest for abstract, task-irrelevant stimuli (resulting in action-associated N1 enhancement), stronger for ecological, but task-irrelevant feedbacks (causing comparable N1 amplitudes for passively viewed and self-triggered pictures) and strongest for behaviorally meaningful stimuli that can be utilized to improve task performance (resulting in N1 reduction). This hypothesis is also consistent with data obtained in healthy participants by Gentsch and colleagues (2012), since feedback signals in their task were crucial for making correct action-effect causality judgments.

4.3 Pictures depicting hands evoke lateralized cortical responses, irrespective of the presence of action

An unexpected finding of Experiment 2 was the hemispheric lateralization of the P1 elicited by left- versus right-hand stimuli, an effect that was independent of our main experimental modulation (PV vs. MI blocks). In particular, pictures depicting the left hand evoked larger P1 amplitudes above the right hemisphere, and the opposite was observed for right hands (Supplementary Figure 3). At first, it is tempting to interpret this result as evidence for lateralization of early visual analysis of human hands to the hemisphere that also controls the movement of that hand (i.e., dominant hand - dominant hemisphere, and vice versa). However, an alternative explanation is that this effect is simply due to low-level image properties, namely, to the asymmetric spatial configuration of our hand stimuli (Figure 1) (Rousselet, Pernet, Caldara, & Schyns, 2011). As mentioned earlier, the visual system seems to be sensitive to the hand laterality, but such effects seem to emerge later, after 150 ms post-stimulus (Stefanics & Czigler, 2012). Therefore, it might be possible that even the P1 is sensitive to hand identity in a lateralized manner, but this idea should be tested systematically, for example, by comparing ERPs elicited by pictures of the dorsal and palmar aspects of both hands. Finally, we found larger N1 amplitudes for right-hand (relative to

left-hand) stimuli above the right hemisphere. This effect can either be due to carry-over from the preceding P1 peak (but in that case, we would have observed the opposite pattern above the left hemisphere) or related to right-lateralized neural responses to body parts (Willems, Peelen, & Hagoort, 2009) and to improved recognition of the dominant hand in right-handed individuals (Ní Choisdealbha, Brady, & Maguinness, 2011).

4.4 Limitations

The contingent paradigm, as utilized in the current study, has several shortcomings, since it does not allow proper experimental control for confounding factors such as temporal attention, nor does it enable the differentiation between non-motor and motor aspects of identity prediction (Horváth, 2015; Hughes et al., 2013b). To account for these issues, Hughes, Desantis and Waszak (2013b) made specific recommendations for future protocols that could have been adapted in the current study. Moreover, the action-response contingency of 50% in our USP blocks is not the most appropriate way for assessing the effect of stimulus predictability, because participants can easily establish predictions about the expected uncertainty of stimulus identity with only two stimuli present (i.e., vertically and horizontally oriented checkerboards, left- and right-hand images). To increase the degree of stimulus unpredictability, it would have been more advantageous to include several stimuli in USP blocks, as it was done previously (Bäss et al., 2008; Hughes & Waszak, 2014). Finally, the inclusion of catch trials would have been important to enhance object-based attention toward feedback stimuli, but also to monitor attentional lapses during the task (Hughes & Waszak, 2011, 2014; Roussel et al., 2014).

4.5 Conclusions

In this study, we report neurophysiological evidence for the presence of sensory attenuation at a very early stage of cortical processing of ecologically valid visual stimuli. We also show that ERPs to self-triggered stimuli are enhanced at subsequent phases of visual analysis, but in addition to the effect of sensorimotor predictive processes, these components are most probably also heavily influenced by

attention. Although we did not find strong evidence for hemispheric lateralization for action-associated ERP modulation, both the P1 and N1 components show some degree of sensitivity to the identity of the hand performing the action. Overall, these ERP modulations can be regarded as automatic and pre-reflective manifestations of processes that can develop into the sense of agency (Synofzik, Vosgerau, & Newen, 2008). Our findings underline the importance of assessing the lateralization of motor-based sensory attenuation in the healthy, because they can contribute to understanding psychiatric conditions such as schizophrenia, which is both characterized by decreased cerebral asymmetry and abnormalities in the awareness of action (Frith, 2012; Sommer, Aleman, Ramsey, Bouma, & Kahn, 2001).

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