A novel experimental paradigm with improved ecological validity reveals robust action-associated enhancement of the N1 visual event-related potential in healthy adults

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Abstract

The association between an action and its sensory consequence has been linked to our sense of agency (SoA). While ecological validity is crucial in investigating such a complex phenomenon, previous paradigms focusing on the cortical analysis of movement-related images used simplified experimental protocols. Here, we examined the influence of action-associated predictive processes on visual event-related potentials (ERPs) in a paradigm that models everyday actions more precisely, using a commercial gesture control device, ecological stimuli depicting a human hand and a behavioural training to reinforce the sense of control over action outcomes. We assessed whether a more natural setup would result in robust ERP modifications following self-initiated movements relative to passive viewing of the same images. We found no compelling evidence for amplitude modulation for the early occipital C1 and P1 components. Crucially, we observed strong action-associated amplitude enhancement for the posterior N1, an effect that was not present in our previous study that relied on conventional button-presses. We propose that the N1 effect in our ecologically more valid paradigm can either reflect stronger attentional amplification of domain-specific visual processes following self-initiated actions, or indicate that sensory predictions in the visual N1 latency range manifest in larger (rather than reduced) ERPs. Overall, our novel approach utilizing a gesture-control device can be a potent tool for investigating the behavioural and neural manifestations of SoA in the visual modality.

Key words: sense of agency, action, prediction, visual ERPs, ecological validity

Highlights

- Action-associated modulations of the visual C1, P1 and N1 ERPs were assessed
- Ecological validity of the paradigm was improved by using a gesture-control device
- The N1 component was larger for movement-induced stimuli
- N1 enhancement following actions seems to be specific to this experimental setup
- Our paradigm offers a new approach to investigate the sense of agency

The sense of agency (SoA) refers to the experience of being the source of self-initiated actions and their sensory consequences [1]. Although, this phenomenon is a central feature of voluntary human actions, its neural underpinnings need further exploration. It is widely accepted that SoA largely depends on the association between an action and its possible outcome. If perceived outcomes match our initial predictions about action-related changes in the sensory environment, SoA is reinforced, which is typically manifested as supressed neural and perceptual responses for self-initiated stimuli [1]. Several studies found that event-related potentials (ERPs) evoked by action-associated stimuli are smaller in healthy adults (a phenomenon commonly referred to as 'sensory attenuation', SA), whereas clinical conditions such as schizophrenia or obsessive-compulsive disorder are characterized not only by aberrant SoA, but also by weaker SA [2, 3, 4].

Although there is converging neuroimaging and electrophysiological evidence for SA for somatosensory and auditory stimuli [5, 6, 7, 8], results obtained in the visual domain are more controversial [9, 10, 11, 12]. Discrepancies between studies focusing on action-associated modulations of visual ERPs might stem from the rather complex interaction between prediction and attention [13], as well as on the degree of the predictability and ecological validity of the stimulus [14].

Ecological validity is a key factor of neurocognitive experiments. Human cognition is extremely complex; therefore, it is crucial that researchers strive to reproduce the features and circumstances of the investigated phenomenon in the laboratory. Numerous paradigms set to investigate action-associated auditory processing used the participants' own voice or touch as stimuli (e.g. [2, 3, 8]). However, the few studies conducted so far in the visual domain fail to demonstrate such a degree of ecological validity: the majority of them involved simplified tasks using abstract stimuli (e.g., checkerboards) evoked by voluntary button-presses [9, 11, 12]. During natural arm movements such as reaching out for an object or gesticulation, we often see our own hand as a visual consequence of the action. Thus, we argue that an experimental setup in which a hand movement is followed by the sight of a hand in such a position that corresponds to the movement, would represent higher ecological validity. Hence, our aim here was to develop a new ERP paradigm that models everyday actions more precisely and therefore, allow studying SoA-associated neural processes in the visual modality. We utilized a gesture-control device complemented with an additional task to induce a stronger sense of control over presented stimuli and to attune the action and the visual outcome. We adapted our previous paradigm [14] and presented ecological stimuli depicting a human hand. To validate this new procedure and to investigate if it elicits stronger ERP modulations to self-initiated stimuli in healthy participants, we analysed three posterior components (C1, P1, N1) arising within 200 ms post-stimulus [15]. We predicted that a more natural setup and a training intended to

enhance SoA over the stimuli would result in enhanced action-associated ERP modifications relative to those reported in studies using conventional button presses and/or abstract visual stimuli.

Twenty-two healthy volunteers (mean age = 26.05 years, SD = 5.68, 11 female) participated in the experiment. Eighteen participants were right-handed, three left-handed, one mixed-handed, as verified by Edinburgh Handedness Inventory [16]. All participants reported normal or corrected-to-normal visual acuity and no history of neurological or psychiatric disorders. The study conformed to 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. Participants were seated 70 cm in front of a 20-inch LCD screen in a dark, sound-attenuated room. The visual stimulus depicting the dorsum of a hand with palm open (congruent with the gender and handedness of the subject; size: 12.2°×8.0°; luminance: 10.7 cd/m^2) was presented for 300 ms using Psychopy 1.801 [17]. The left-hand stimulus was the mirror image of the right-hand stimulus. A red fixation cross (size: 0.6°) was always present at the centre of the screen and participants were asked to maintain fixation throughout the experiment.

We used a Myo armband (Thalamic Labs, Kitchener, Canada) to facilitate the participants' feeling of ownership towards the stimuli (Figure 1). The Myo armband is a wireless device, enabling users to control technology by using a set of sensors: eight electromyographic (EMG) sensors detect muscle activity of the forearm, while a 9-axis inertial measurement unit (IMU) is responsible for identifying the orientation and the movement of the arm. The armband streams EMG and IMU data at 200 Hz and 50 Hz to the computer via Bluetooth Low Energy.

We adopted the contingent paradigm with three conditions: passive viewing (PV), motor-induced (MI), and motor-only (MO), 120 trials in each. During PV, stimuli appeared with randomized interstimulus interval (ISI) of 1500-2450 ms (with 50 ms steps, 20 ISIs in total) while participants were asked to maintain fixation. In MI blocks, participants were required to perform wrist dorsiflexions in a self-paced manner, aiming at a rhythm of about 2 seconds. Participants were instructed that the software would not respond to fast responses (<1500 ms, unbeknownst to the participants) and that each movement would be immediately followed by a briefly presented hand stimulus. In MO blocks, subjects had to produce self-paced movements identical to those in the MI task, but no stimulus would appear on the screen (Figure 1A). In the MI and MO conditions, EEG markers were sent out when the muscle contraction of the forearm reached a certain, individually calibrated threshold. In the PV condition, EEG markers were synchronized to the end of the predetermined ISI, preceding the onset of new stimulus by one frame (16.6 ms). In MI and PV blocks, stimuli also appeared with exactly one frame delay following the EEG marker, allowing direct comparison of ERPs obtained in the two conditions. Conversely, markers were synchronized to the

EMG-monitored onset of actions, enabling to calculate MI-MO difference waveforms to control for movement-related EEG signals.

We included a fourth, 'reinforcement of control' (RoC) condition to develop strong SoA over the hand stimulus. These trials started with the presentation of a red square (size: 2.46°× 2.46°) appearing at random screen locations (Figure 1B). The participants' task was to 'grab' the square by moving the hand stimulus over the square on the screen such that they would control stimulus movement by moving their hands. Once the stimulus covered the square, they had to make a fist by flexing their fingers, which would trigger the replacement of the hand stimulus with an image of a fist of the same hand (size: 9.2° × 6.2°). At the same time, the red square disappeared, and a new trial was initiated by the appearance of the target square at another location. There were no time constraints for this task, but participants were asked to 'grab' each square as fast and accurately as possible. The RoC task was performed before each of the three experimental conditions with 20 trials each. Additionally, single RoC trials were presented unexpectedly during PV, MI and MO blocks, after every 15^{th}-21^{st} trial (resulting in 6-8 RoC trials per block). EEG collected in RoC trials was not analysed. The scripts used for armband calibration, action-stimulus reinforcement (RoC block), stimulus presentation and sending out EEG markers (PV, MI and MO blocks) and are available at https://github.com/6uliver/myo-module-for-erp-studies-on-soa/.

The duration of PV blocks was around 6 min, whereas MI and MO blocks lasted for about 6–9 min, depending on individual response times. Participants could have a short rest between the blocks. MO and MI blocks started with a short practice that consisted of at least 15 trials, and lasted until the timing of dorsiflexions exceeded 1500 ms on >80% of trials. During the practice, participants got immediate feedback about their response times to get acquainted with task requirements. The duration of the whole experiment was about 1 hour, while the tasks (3 experimental plus 3 RoC blocks) lasted for about 30 min.

EEG was recorded with a BioSemi ActiveTwo Amplifier (BioSemi, Amsterdam, The Netherlands) at a sampling rate of 1,024 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, O2). In addition, two electrodes were placed at the outer canthi of both eyes to record horizontal eye movements. Artifacts related to vertical eye movements (blinks) were monitored at electrodes Fp1 and Fp2. The recording reference and the ground electrodes (common mode sense and driven right leg electrodes in the ActiveTwo system) were placed in close proximity to the Cz position. Data were collected without applying frequency filters.

EEG was analysed with the EEGLAB [18] and ERPLAB [19] toolboxes for MATLAB (MathWorks, Natick, MA). EEG markers in all experimental conditions were shifted by 16.6 ms to correct for the delay of stimulus presentation. Continuous EEG was band-pass filtered between 0.5–30 Hz using an infinite impulse response Butterworth filter (12 dB/oct). Epochs with 100 ms pre- and 600 ms post-stimulus were extracted. Epochs containing baseline fluctuations, muscle and horizontal eye movement-related artefacts were removed manually, yielding at least 110 artefact-free epochs for all participants and stimulus conditions. Ocular artefacts were removed with independent component analysis. Further, sinusoidal noise stemming from AC power line fluctuations (50 Hz line noise + harmonics) was removed with the CleanLine plug-in for EEGLAB. Data were re-referenced to Fz electrode, and epochs corresponding to each experimental condition were averaged. ERPs obtained in the MO block (containing neural activity associated with motor preparation and execution) were subtracted from MI data of the same participant, resulting in "corrected motor-induced" (C-MI) difference waveforms. Thus, we could compare PV and C-MI data 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 68–78 ms, 86–126 ms, and 160–180 ms time windows, respectively. These intervals were selected to centre around the peak of each component on the waveform averaged across all participants and experimental conditions.

The effect of CONDITION (PV vs. C-MI) and its potential interaction with ELECTRODE location (for the P1 and N1 components) was tested with Bayesian repeated-measures ANOVA implemented in JASP 0.9.2, using default prior scales [20]. In contrast to conventional null hypothesis significance testing (NHST), Bayesian statistics enable the estimation of evidence favouring either the alternative or the null hypothesis using Bayes Factors (BFs, $BF_{10} > 3$ and $BF_{10} < 0.33$ indicating at least moderate evidence favouring the former and the latter, respectively). To enable comparison with previous reports using NHST, we also performed repeated-measures analysis of variance (ANOVA) with CONDITION and ELECTRODE (if applicable) as within-subject factors. Significance level was set to .05; Greenhouse-Geisser-corrected F and *p* values are reported if the assumption of sphericity was violated. Effect size (η_p^2) was also calculated.

Grand-averaged ERP waveforms, bar plots representing modulations in ERP amplitudes across experimental conditions, and posterior scalp distributions of the PV -vs. C-MI difference waveforms are presented in Figure 2. Analysis of the C1 component indicated no evidence for movement-induced amplitude modulation (main effect of CONDITION: $BF_{10} = 1.11$, $F(1,21) = 2.98$, $p = .099$, $\eta_p^2 = .12$). For the P1 component, there was moderate evidence for increased amplitude following self-initiated actions (CONDITION: $BF_{10} = 3.69$), but NHST did not indicate a significant

main effect ($F(1,21) = 1.65$, $p = .213$, $\eta_p^2 = .07$). Furthermore, we found no interaction between CONDITION and ELECTRODE ($BF_{10} = 0.14$, $F(2,42) = 1.04$, $p = .362$, $\eta_p^2 = .05$). Finally, there was strong evidence for enhanced N1 amplitudes for movement-induced stimuli (CONDITION: $BF_{10} = 57796.15$, $F(1,21) = 27.61$, $p < .001$, $\eta_p^2 = .57$), and this effect was comparable above the two hemispheres (CONDITION x ELECTRODE: $BF_{10} = 0.3$, $F(1,21) = 0.31$, $p = .585$, $\eta_p^2 = .01$).

Our new paradigm with improved ecological validity revealed robust action-associated N1 enhancement above both hemispheres. The posterior N1 (or N170) component is sensitive to the presentation of faces and body parts [21, 22], and has been associated with activity in domain-specific modules of the visual system [23, 24]. From this perspective, it is not surprising that the N1 was the waveform showing the strongest movement-related modulation in the current study. Given that ERP amplitude enhancements are often associated with attention [11, 12, 13, 14], stronger attentional amplification of visual analysis in the MI condition is a probable underlying mechanism for the N1 effect. Although top-down predictive processes seem to modulate the amplitude of the N1 in the opposite direction, with smaller N1 components representing a stronger correspondence between expected and encountered stimuli [4, 13, 25, 26, 27], previous studies in the visual modality also found enhanced amplitudes connected to voluntary actions [11, 12]. Still, in our prior study, we found the N1 to be insensitive to self-initiated presentation of stimuli depicting a human hand, albeit that the paradigm relied on a more conventional setup with button presses, and did not include a RoC condition to reinforce the association between movements and their sensory consequences [14]. Taken together, the larger N1 component in our MI condition with the current experimental setup might either reflect stronger attentional amplification of visual processing [11, 12], or point toward the notion that movement-related predictive processes in the visual domain increase rather than suppress the posterior N1. The current design, however, does not allow the differentiation between these two possible explanations; thus, further studies, applying systematic task manipulations, are needed. Either way, our finding on the N1 can be viewed as the manifestation of action-associated modulation of intermediate-level visual processing that is both sensitive to the category of the stimulus and to the dynamic context in which it is being encountered.

Despite our expectations [14], we did not find compelling evidence for C1 reduction and P1 enhancement for movement-induced stimulus presentation. To account for these negative findings, we consider the possibility that by designing a protocol with improved ecological validity, ERP effects observed in our previous study (affecting the C1 and P1 components, [14]) shifted forward in time and influenced later stages of visual analysis (i.e., the P1 and the N1).

Overall, the present paradigm consisting of a gesture-control device combined with a short training seems to be a potent tool for investigating the mechanisms underlying action-related

modulation of visual processes, especially those associated with higher-level analysis of the sensory environment. Our approach can facilitate research towards understanding the behavioural and neural manifestations of SoA across a wide range of experimental setups, both in healthy populations and in clinical conditions such as schizophrenia and obsessive-compulsive disorder. Future work should aim to achieve even greater ecological validity by precisely modelling real-life actions in a controlled environment, e.g., utilising gesture-control devices in virtual reality.

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Declaration of interest

The authors have no financial or personal conflicts of interest. After finishing the study, the authors informed Thalamic Labs about the results, who provided a Myo Armband device to support future research.

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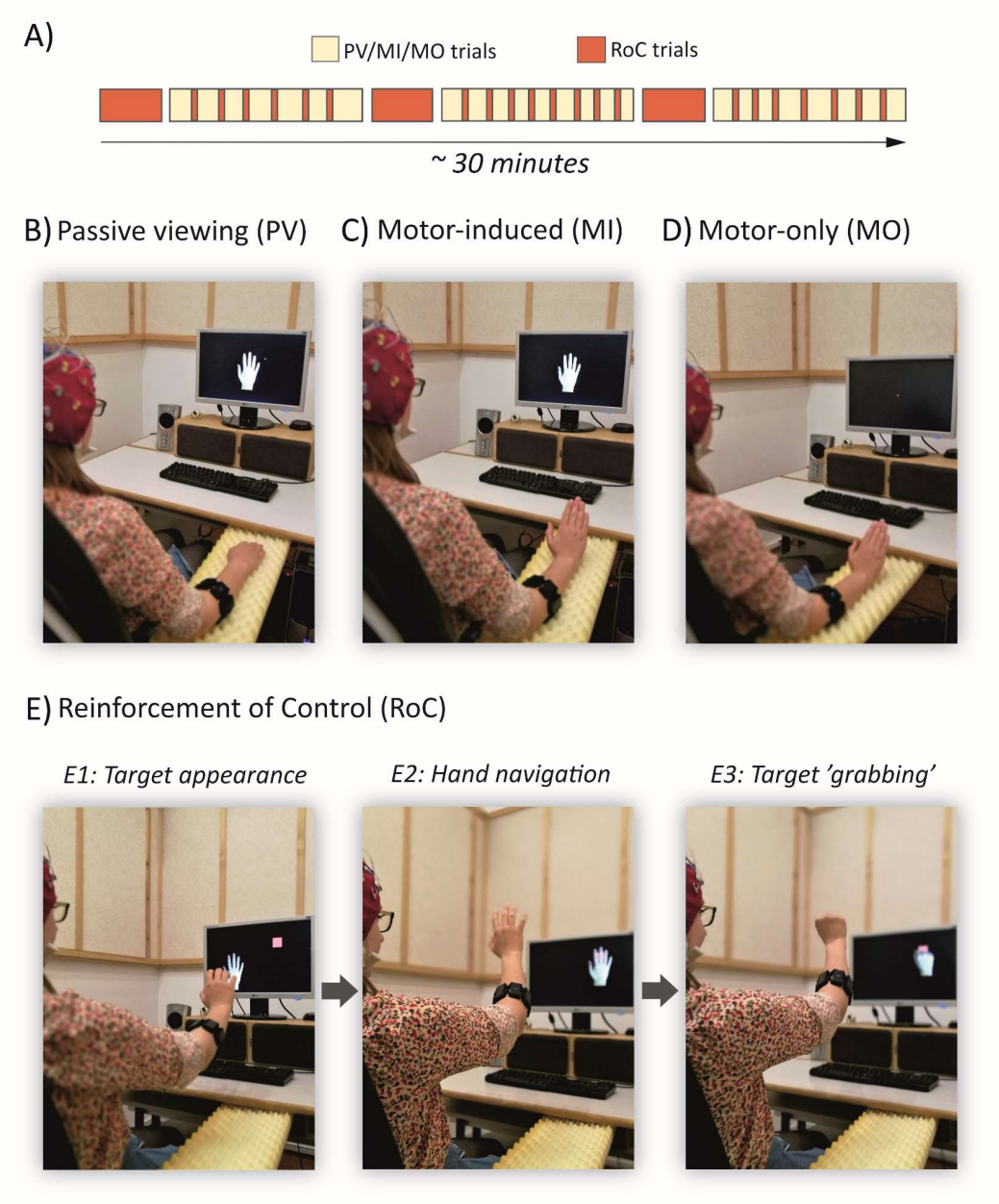

Figure 1. (A) Overview of the experimental protocol. Trials for conditions PV, MI and MO (yellow lines) were presented in separate blocks (counterbalanced order across participants), each being randomly interrupted by single RoC trials (vertical red lines). Each block was preceded by a RoC training consisting of 20 trials (long red lines). (B-D) Visual depiction of the three experimental conditions used to collect EEG data. Conditions PV and MI consisted of identical visual stimuli, whereas conditions MI and MO were characterized by identical motor requirements. (E) The structure of RoC trials: after the appearance of a red square (target; E1), participants were required to navigate the hand stimulus above it by moving their arms (E2), and to 'grab' the target by making a fist (E3), which would trigger the disappearance of the target. MI = motor-induced, MO = motor-only, PV = passive viewing, RoC = reinforcement of control

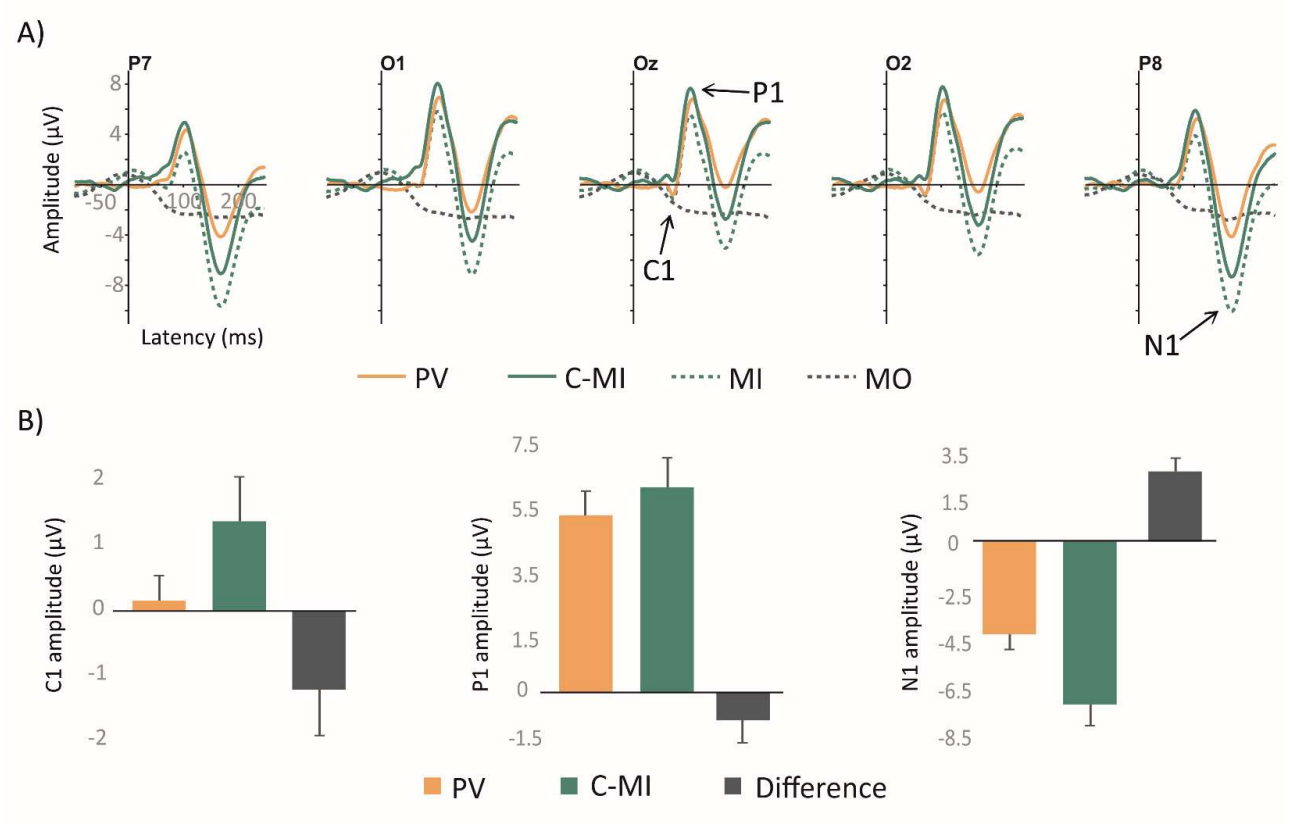

Figure 2. (A) Visual event-related potentials recorded at five posterior scalp locations on waveforms from our three experimental conditions (PV, MI, MO) as well as on the MI – MO difference waveform (C-MI). (B) C1, P1, and N1 ERP amplitude data (means and standard errors of Oz, O1/Oz/O2, and P7/P8 electrodes, respectively) extracted for the PV, C-MI and PV – C-MI waveforms. C-MI = corrected motor-induced condition; MI = motor-induced, MO = motor-only, PV = passive viewing