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Prismatic adaptation modulates oscillatory EEG correlates of motor preparation but not visual attention in healthy participants

Prism-induced effects on brain oscillations

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Abstract

Prismatic adaption (PA) has been proposed as a tool to induce neural plasticity and is used to help neglect rehabilitation. It leads to a recalibration of visuo-motor coordination during pointing as well as to after-effects on a number of sensorimotor and attention tasks, but whether these effects originate at a motor or attentional level remains a matter of debate. Our aim was to further characterise PA after-effects by using an approach that allows distinguishing between effects on attentional and motor processes. We recorded electroencephalography (EEG) in healthy human participants (9 females and 7 males) while performing a new double step, anticipatory attention/motor preparation paradigm before and after adaptation to rightward shifting prisms, with neutral lenses as a control. We then examined PA after-effects through changes in known oscillatory EEG signatures of spatial attention orienting and motor preparation in the alpha and beta frequency bands. Our results were twofold. First, we found PA to rightward shifting prisms to selectively affect EEG signatures of motor but not attentional processes. More specifically, PA modulated preparatory motor EEG activity over central electrodes in the right hemisphere, contralateral to the PA-induced, compensatory leftward shift in pointing movements. No effects were found on EEG signatures of spatial attention orienting over occipito-parietal sites. Second, we found the PA effect on preparatory motor EEG activity to dominate in the beta frequency band. We conclude that changes to intentional visuo-motor rather than attentional visuo-spatial processes underlie the PA after-effect of rightward deviating prisms in healthy participants.

Keywords: prismatic adaptation (PA), after-effect, motor preparation, attention orienting, electroencephalography (EEG), brain oscillations

Significance Statement

Prismatic adaptation (PA) has been proposed as a tool to induce neural plasticity in both healthy participants and patients, due to its after-effect impacting on a number of visuo-spatial and visuo-motor functions. However, the neural mechanisms underlying PA after-effects are poorly understood as only little neuroimaging evidence is available. Here, we examined for the first time the origin of PA after-effects studying oscillatory brain activity. Our results show a selective modulation of preparatory motor activity following PA in healthy participants but no effect on attention-related activity. This provides novel insight into the PA after-effect in the healthy brain and may help to inform interventions in neglect patients.

Introduction

Following a right-hemispheric lesion, patients often show visuo-spatial attention and motor-exploratory biases away from contra-lesional hemispace (Benton and Tranel, 2003; Vallar, 1998). Neglect is usually difficult to treat but some of the lateralized deficits are alleviated by prismatic adaptation (PA) (Rossetti et al., 1998), which combines a visuo-motor pointing task with prisms that displace the visual image right- or leftwards. Thus, when pointing while wearing prismatic goggles, participants initially mispoint in the direction of the prismatic shift, experiencing a visuo-proprioceptive mismatch between their movement and the actual target position. Within few trials, participants are able to adapt their movement to the new visuo-motor contingencies and to compensate for the erroneous bias. As a consequence of this sensorimotor realignment, pointing movements are biased in the direction opposite to prism deviation when goggles are removed, the so-called prism after-effect of clinical interest (Pisella et al., 2006).

Interestingly, the prism after-effect is not merely a sensorimotor phenomenon but also extends to more complex cognitive domains (review in Michel, 2016). Numerous studies in healthy controls and neglect patients have reported PA after-effects on a variety of tasks, including line bisection (Pisella et al., 2002; Schintu et al., 2014), visual search (Vangkilde and Habekost, 2010), endogenous and/or exogenous orienting of attention (Nijboer et al., 2008; Striemer and Danckert, 2007; Striemer and Danckert, 2010a), spatial/temporal representation (Bultitude et al., 2013; Rode et al. 2010; Magnani et al., 2010; 2011; 2013; Oliveri et al., 2013) and visually guided actions (Striemer and Danckert, 2010b).

While behavioural effects of PA have been investigated in detail, its underlying mechanisms are still debated. The most prominent account is that PA affects visuo-spatial attention and visuo-motor functions by acting on the dorsal stream (Striemer and Danckert, 2010a). In line with this hypothesis, neuroimaging studies revealed bilateral activation of parietal and cerebellar areas during the error detection and error correction phase of prismatic adaptation regardless of prism direction (Chapman et al., 2010; Clower et al., 1996; Danckert et al., 2008; Luauté et al., 2006; 2009). The only fMRI-study testing PA after-effect reported opposite co-modulation of parietal activity over the two hemispheres during a visual detection task (Crottaz-Herbette et al., 2014).

More recently, the involvement of the primary motor cortex (M1) in PA after-effects has also been documented. Using TMS, Magnani et al. (2014) reported increased intracortical facilitation in M1 contralateral to the prism-induced compensatory shift for both left- and rightward deviating prisms. M1 involvement could be a consequence of PA-induced changes in areas connected to M1. For instance, it is conceivable that PA affects M1 via modulating parietal-M1 interactions (Schintu et al., 2016), or via its connections to the cerebellum, the latter being essential for PA as suggested by fMRI in healthy participants (Crottaz-Herbette et al., 2014, Danckert et al., 2008; Küper et al., 2014) and studies in cerebellar patients who exhibit a reduction of the prismatic after-effect (Pisella et al., 2005; Weiner et al., 1983).

Collectively, the literature therefore indicates that PA acts on dorsal stream function but it is unclear whether it predominantly affects attention-related or motor-related dorsal stream processes, or both. In the present study, we aimed to further probe the origin of the PA after-effect by examining EEG changes after adaptation to rightward-deviating prisms, while healthy participants performed a task involving covert attention orienting to the left or right visual field, followed by preparation of a left or right hand motor response in the same trial. Our analyses focused on well-known EEG-signatures of lateralized anticipatory attention orienting and motor preparation, namely asymmetric changes in occipito-parietal alpha-activity (Foxe and Snyder, 2011; Thut et al., 2006; Worden et al., 2000) or rolandic mu-/beta-activity (Kilavik et al., 2013; Pfurtscheller and Lopes Da Silva, 1999; Tan et al., 2013) to distinguish between PA after-effects on attentional visuo-spatial and intentional motor processes respectively.

Material and methods

Participants

Sixteen healthy adults (9 females, 7 males, mean age = 25.62 years, SD = 4.47) volunteered to participate in this experiment. All participants were right handed, had normal or corrected-to-normal vision and reported no history of neurological or psychiatric disease. Participants were financially compensated for taking part in the study. Signed informed consent was obtained from each participant at the beginning of the experiment, which was carried out at the Institute of Neuroscience and Psychology, University of Glasgow. The study was performed in accordance with the Declaration of Helsinki, and was approved by the ethics committee of the College of Science and Engineering, University of Glasgow.

Paradigm, procedure and apparatus

Participants performed a new double step anticipatory attention/motor preparation paradigm involving in the same trial anticipatory attention to lateralized positions (symbolically cued orienting of visual-spatial attention), followed by lateralized motor preparation (with a delayed response component). In this task, a first, attentional cue guided the focus of spatial attention, while a second, motor preparation cue signalled whether a right or left hand movement had to be prepared. The two, successive post-cue intervals (of 1.5 sec each) allowed to assess the EEG correlates of anticipatory attention deployment and motor preparation towards the left versus right space respectively, namely by analysing changes in posterior alpha and rolandic alpha/beta oscillations, our primary EEG measures of interest. Because the motor cue was presented at validly cued/ attended and invalidly cued/ unattended positions, it also served as visual target, allowing the assessment of attentional effects on both behavioural and post-stimulus EEG measures (i.e. behavioural responses and visually evoked potentials to the targets).

All participants took part in one training session and two experimental sessions, each on a separate day. One experimental session involved prism adaptation (using prismatic lenses), while in the other experimental session control (neutral) lenses were used. During the training session not involving any EEG recordings, participants were familiarized with the behavioural (attention/motor) task. This session also served for target titration. During the experimental sessions (**Fig. 1A**), participants were first prepared for EEG recordings (EEG set-up). They then performed two blocks of the behavioural task lasting around 8 min each, while EEG was recorded (2x EEG - task). These two blocks served as baseline for attentional and motor preparatory EEG signatures. Afterward, participants underwent prismatic adaptation using prismatic or neutral lenses (PA - rightward or neutral lenses). After PA, EEG was again recorded while participants performed the same behavioural task for two further blocks (2x EEG - task), which served to assess PA after-effects on the EEG signatures of interest. The order of the two experimental sessions was randomized across participants.

Attentional/motor task, experimental design and analysis of behavioural data.

Stimuli were presented on a CRT monitor with a 1280 x 1024 pixel resolution, a 100 Hz refresh rate and a grey background using E-Prime (Psychology Software Tools, Pittsburgh, PA).

Fig. 1B illustrates the stimuli and the sequence of events per trial. Each trial began with the presentation of a central fixation cross (1.5° visual angle) inscribed into a rhombus (2x2°). Together with the central rhombus, two lateralized rhombi (3.5x3.5°) serving as placeholders were continuously displayed in the lower left and right visual fields. After 1500ms from trial onset, either the bottom left or the right section of the central rhombus turned green for 30ms. This served as the attentional cue instructing the participants to covertly shift and maintain their attention towards the left or right placeholder, respectively. After 1500ms, a left or right segments of either placeholder turned black for 40ms (in 80% of trials at validly cued and in 20% of trials at invalidly cued position), serving both as the visual target (to assess attentional effects in both behavioural and EEG data, see below) as well as the motor preparation cue, as its form (left or right-pointing triangle) indicated which hand the participants had to use for the upcoming motor response (see Fig 1B: upper right insets for examples of motor cues). For motor cueing, the direction of the arrow pointed equally often left and rightward (50% of trials) irrespective of the side of the placeholder the motor cue was presented in. Participants were instructed to prepare a left or right index finger movement according to the motor cue direction as soon as this appeared, but were asked to withhold the response for 1500ms, until the fixation cross turned into a green vertical line for 30ms (go signal). To encourage movement preparation before the go-signal, speeded response execution was emphasized and a red cross was presented in the central rhombus as a warning signal if no response occurred within the first 500ms after the go-signal, in which case the trial was aborted and a new trial started.

The task consisted of a total of 232 trials pre- and 232 trials post-PA, divided into 2 blocks of 116 trials each (Fig. 1A). In 200 out of the 232 trials per pre-/post-blocks, we presented large attentional targets/motor cues that covered a full half of the placeholder (Fig 1B, upper right insets). In the remaining 32 trials, we employed smaller attentional targets/motor cues that consisted of small left or right segments of the placeholder rhombi turning black (see Fig 1B, upper far right insets), leading to small left or rightward pointing triangles (0.5° visual angle), and which were presented in 50% of trials at validly cued and 50% of trials at invalidly cued positions. For these small targets, luminance contrast with the background was titrated during the training session for each participant to give rise to peri-threshold performance with a behavioural advantage for cued stimuli compared to uncued stimuli (mean detection accuracy valid trials = .75; invalid trials = .55). Using this design, we could control via behavioural measures inferred from the small-target/cue trials that participants shifted attention as instructed (because small stimuli were not at ceiling, i.e. led to clear attentional benefits/costs), and at the same time had enough large-target/cue trials (n=100 per smallest condition cell) to analysis EEG with a good signal-to-noise ratio (small target/cue trials were excluded from EEG analysis because difficult to perceive and hence likely associated with uncertainty about what hand to choose for motor preparation).

Participants were seated on a comfortable chair at a distance of 57 cm from the screen. The distance was kept constant throughout the session using a chin rest. Participants were instructed to keep their eyes on the fixation cross throughout the experiment, shift their attention in response to the attentional cue without moving their eyes and to prepare but withhold the speeded motor response until the go signal appeared. Participants responded with their left or right index finger by a button press on a keyboard, according to the direction indicated by the motor cue.

Analysis of behavioural data: Data were analysed separately for “small” and “large” target stimuli. Responses to small targets were analysed in terms of accuracy as a function of valid and invalid attentional cueing in order to ensure that participants engaged in the attention task. Responses to "large" targets were analysed in terms of accuracy and reaction times for providing (descriptive) information on how well participants prepared for the motor response.

Prismatic adaptation (PA) and analysis

We employed a non-automated, single-blinded PA procedures as previously described (see e.g. Magnani et al., 2010, 2011, 2013, 2014; Oliveri et al., 2013). Non-automated procedures are extensively used in the clinical setting with patients, and the procedure we employed has been widely used in research including healthy participants (Calzolari et al., 2015; Làdavas et al., 2011; Magnani et al., 2014; see for other non-automated PA procedures: Crottaz-Herbette et al., 2014; Martín-Arévalo et al., 2016; O'Shea et al. 2017). Participants were seated in front of a curved, horizontal plexiglass panel (height: 30 cm, width: 72 cm, depth: 34 cm at the centre and 18 cm at the periphery, distance from participant: 57 cm). The panel was placed on a table top between the participant and the experimenter. The concave side was facing the participant and the convex side the experimenter. The panel was transparent and graded with thin vertical lines per degrees of visual angle (120° of visual angle covered), so that the experimenter could readout the participants' pointing accuracy per trial: rightward pointing deviations from a target were scored with positive values, leftward ones with negative values.

During PA, the experimenter placed a visual target (a pen) at the top of the surface of the transparent barrier (tipping the pen on its top edge) in one of three possible positions (randomly determined on each trial): a central position (0°), 11° to the left and 11° to the right of centre. At the start of each trial, participants were asked to keep their right hand at the level of the sternum and upon target presentation to position their finger tip on the panel at target eccentricity, at a fast but comfortable speed. The experimenter recorded spatial accuracy of pointing as distance in degrees of visual angle between the target position and the final position of the participant's finger.

The pointing task consisted of a total of 180 trials (i.e. 60 trials for each target position) and was subdivided in three main stages: pre-exposure, exposure and post-exposure, with pre-exposure and exposure each subdivided into two further stages, leading to a total of five PA stages (**Fig. 2**). Pre-exposure consisted of 60 trials (20 trials for each pointing position). Participants performed half of the pre-exposure trials (i.e. 30) with visible pointing (pre-exposure free-viewing), and half (i.e. 30) with invisible pointing (pre-exposure blinded). During blinded pointing, the view of the arm movement and panel was occluded by means of a cape that covered the area from neck to the edge of the panel (neither obstructing the pointing movements, nor the visibility of the top edge of the panel or the target position). During exposure, participants performed the task while wearing rightward-deviating prismatic or neutral goggles. The prisms induced a 10° shift of the visual field to the right. During exposure, participants could always see the trajectory of their movement (visible pointing) and were asked to point 90 times to targets (i.e. 30 trials per position). In the early phases of exposure (early exposure, see Fig 2), pointing movements are typically observed to deviate to the right (with rightward-deviating goggles). In later exposure phases, this is typically compensated for by adaptation (late exposure/ adaptation, see Fig 2). In the post-exposure phase, the strength of adaptation was assessed by measuring the after-effect (usually leftward, compensatory pointing after rightward prisms) during invisible pointing (pointing movements occluded) in 30 trials (10 per target position). To limit de-adaptation, participants were instructed to keep their eyes closed between prism adaptation and EEG after-effect evaluation (post-exposure invisible pointing), i.e. before starting the attention/motor task.

Analysis. In order to probe for prismatic adaptation effects, we assessed pointing deviation from the target in visual degrees in all 5 stages: pre-exposure free-viewing, pre-exposure blinded, early exposure, late exposure/adaptation, post-exposure/after-effect. For exposure, the first and second half of trials were analysed separately, because these are typically associated with differential effects when prismatic lenses are used (early rightward bias with rightward lenses, later compensation for this bias) (e.g. Magnani et al., 2014). To statistically test for PA effects with prismatic lenses as compared to neutral lenses, we conducted a 2 x 5 repeated-measures ANOVA with Exposure Type (Prism *vs.* Neutral) and Time (5 PA phases) as within-subjects factor. Simple tests were conducted to break down main effects and interaction where appropriate.

EEG recording and pre-processing

EEG was continuously recorded during the task with 1000 Hz sampling rate from 62 Ag/AgCl sintered electrodes mounted on an elastic cap according to the International 10-10 system (BrainAmp, Brain Products GmbH, Munich, Germany). An additional electrode was positioned on the outer canthus of the left eye to record eye movements (when referenced to Fp1), while AFz and TP9 served as reference and ground, respectively. All impedances were kept below 5 kΩ.

EEG data were analysed using BrainVision Analyzer2 (BrainProducts) and FieldTrip toolbox (Oostenveld et al., 2011; http://www.ru.nl/fcdonders/fieldtrip/) in Matlab 7 (MatWork, MA). EEG was bandpass filtered offline from 0.5 to 80 Hz and re-referenced to the average of all channels. A band-stop filter was then used to remove 50 Hz activity. An independent component analysis (ICA) was performed to remove eye blinks and muscle artefacts. EEG data were then segmented into 4000ms epochs, starting 1000ms before and ending 3000ms after the first (attentional) cue (hence spanning 1500ms into the post-motor cue period). Based on visual inspection, trials with further artefacts were rejected. Trials with small motor cues were not included in the EEG analysis. Finally, data sampling rate was reduced to 512 Hz for analysis.

The experimental design gave rise to 200 EEG trials for each of the four main conditions (Pre *vs.* Post x Prism *vs.* Neutral lenses), equally divided in 100 left- and 100 rightward pointing attentional cues, and 100 left- and 100 rightward pointing motor cues. From this set of trials, we discarded on average 9% of trials due to errors, slow responses and EEG artefacts (9%±5.3). Analyses were therefore based on averages of n=91 trials per smallest condition cell (left- or rightward orienting, and left or right hand motor preparation).

EEG: Time frequency analyses

For each participant, condition and trial, time-frequency analyses were performed using Fast Fourier transform for all frequencies ranging from 2 to 40Hz, using a Hanning taper with a fixed 500ms sliding time window moving in steps of 20ms. The power was averaged over trials for each block of recording (pre/post Prism, pre/post Neutral). Analyses were separated to cover the epochs of anticipatory attention shifts (i.e. –200 to +1500ms from the attentional cue onset) and of motor preparation respectively (i.e. -200 to +1500ms from motor cue onset). No baseline correction was applied for analysis in the frequency domain. The analyses were performed on the EEG correlates of either attention orienting or motor preparation in two steps, i.e. using (1) a nonselective cluster based analysis taking into account the whole scalp data, and (2) a planned analysis within electrodes of interest (EOIs). Both analyses were inspired by prior literature (see for a recent example in Marshall et al., 2015). Note that analysis 1 did not inform analysis 2 at any stage, and hence were performed independently.

EEG correlates of attentional shift. For each participant, condition and time point, trials were averaged separately for attentional left and attentional right cues. Data were examined for EEG indices of attentional modulation by contrasting attention right and attention left trials ($Power_{\text{Attention right}} - Power_{\text{Attention left}}$) per electrode (as in e.g. Marshall et al. 2015) which were then interrogated in regards to differential changes across conditions (see statistical analyses below). In order to normalize data, a common denominator was created to divide the data by the average over attention left and right trials of all conditions (as in Marshall et al. 2015), consisting here of exposure type (Prism and Neutral condition) and time (pre and post PA). To evaluate prismatic adaptation effects on attention, EEG analysis focused on activity between 8-12Hz. This frequency band was pre-defined in line with many previous studies reporting modulation of posterior alpha-activity with spatial attention deployment (for review see e.g. Foxe and Snyder, 2011; for examples see Worden et al., 2000; Thut et al., 2006).

EEG correlates of motor preparation. For each participant, condition and time point, trials were averaged separately for left and right motor preparation cues. Data were then analysed in terms of differential motor preparatory signals between left and right hand preparatory trials ($Power_{\text{Right Hand}} - Power_{\text{Left Hand}}$) per electrode across conditions, in analogy to the analysis described above. Again, a common denominator was calculated in order to normalize data by dividing by the average over motor left and right trials across all conditions, i.e. exposure types (Prism and Neutral) x time (pre- and post-PA). We analysed activities in both the alpha/mu (8-12Hz) and beta band (16-25Hz), as both these frequency bands are known to be modulated by unimanual motor preparation over rolandic sensors (Kilavik et al., 2013; Pfurtscheller and Lopes Da Silva, 1999; Tan et al., 2013).

Statistical analyses. Statistical analyses on the above data were conducted separately for attentional and motor cue periods and frequency bands of interest (alpha and beta bands) as follows in two steps.

First, we set up a cluster-based permutation statistics including all electrodes (Maris and Oostenveld, 2007) in order to probe the interaction effect of interest, namely a differential effect of intervention (Pre *vs.* Post) depending on exposure type (Prism *vs.* Neutral lenses) on the attention orienting and/or motor preparatory signals. The cluster based statistics was computed over the time periods from 200-1000ms for the attentional cue period, and 500-1200ms for the motor preparatory period in the respective frequency ranges of interest (8-12Hz, 16-25Hz). For the cluster based statistics, dependant-sample t tests were run for the contrasts of interest, i.e. either on Post minus Pre Prism *vs*. Post minus Pre Neutral (for exploring the interaction between Exposure Type (Prism *vs*. Neutral) by Time (pre *vs*. post)) or on Post Prism *vs*. Pre Prism as well as Post Neutral *vs*. Pre Neutral (for exploring the associated simple effects of Time per Exposure Type when appropriate). Clusters of adjacent data points in space were defined by means of a clustering algorithm using a threshold of $p < .025$ (two-sided t-test). The cluster-level test statistic was defined from the sum of t values of the sensors in a given cluster. Finally, clusters were evaluated in terms of statistical significance against a permutation distribution, obtained by 2500 permutations of randomly shuffling the conditions within all participants.

Second and in line with previous studies, we run an additional analysis calculating modulation indices by attention orienting/ motor preparation over posterior and central EOIs (previously shown to reliably capture spatial attention deployment and motor preparation respectively; e.g. Thut et al., 2006; Marshall et al. 2015; Vukelić et al., 2014; Wang et al., 2017). An attentional modulation index (AMI) and a motor preparation index (MPI) were calculated per hemisphere by averaging EEG power changes over electrodes of interest. EOIs were defined as the groups of electrodes in either the left or right hemisphere that showed the strongest average alpha/beta modulation by attention orienting/ motor preparation when collapsed across all conditions (see also Marshall et al., 2015). In analogy to previous literature, these electrodes corresponded to posterior, occipito-parietal electrodes for calculation of the attention orienting index (P3/P5/P7/PO3/PO7/O1, P4/P6/P8/PO4/PO8/O2) and central electrodes for the motor preparation index (C3/CP3, C4/CP4). AMI and MPI were then calculated according to the formula: ($Power_{\text{Contralateral}} - Power_{\text{Ipsilateral}}$)/[*Common Denominator*] (Marshall et al., 2015), where contralateral and ipsilateral refer to the attentional focus with respect to the electrodes of interest for the AMI, and to the hand the participants were instructed to move for the MPI. The Common Denominator refers to the average of contralateral versus ipsilateral changes across all conditions, i.e. exposure type (Prismatic and Neutral condition) and time (Pre and Post PA). For both AMI and MPI, positive index values indicate a modulation of power in the direction expected from prior studies on attentional orienting and motor preparation, namely a contralateral decrease and ipsilateral increase in power (in which case both numerator and denominator are negative). This index therefore indicates the degree of modulation observed within each hemisphere, allowing to test per hemisphere whether PA affected these modulations (the index would converge to 0 if there were no difference in power between contra- and ipsilateral conditions). We probed whether the AMI and/or MPI are differentially affected by intervention (Pre vs Post) depending on Exposure Type (Prism vs neutral) and hemisphere using a repeated measure ANOVA with factors Exposure Type (Prism *vs*. Neutral), Time (Pre *vs*. Post) and Hemisphere (Left *vs*. Right).

Bayes factor (BF) analysis

To further inform the interpretations of our results, we calculated a BF for all statistical comparisons pointing to a null effect ($p > .05$) (Rouder et al., 2009). Unlike inferential statistics, which do not provide information about the null hypothesis, the Bayesian approach allows a quantification of how strong the evidence is for the alternative or the null hypothesis. To this end, we compared the magnitude of the PA-induced effects (post-PA minus pre-PA) to changes occurring in the Neutral condition (post-Neutral minus Pre-Neutral). Our alternative hypothesis was that changes induced by PA (post-PA minus Pre-PA) are significantly different from the neutral condition, whereas the null hypothesis was that the two conditions are equivalent. Specifically, the BF was estimated setting the prior on effect size following a Cauchy distribution with a scale factor 1 (Rouder et al., 2009). Despite the fact that evidence is continuous, $B < 1/3$ can be considered as strong evidence in favor of the null hypothesis, $B > 3$ as strong evidence in favor of the alternative hypothesis, whereas $1/3 < B < 3$ indicates data insensitivity (i.e. support for neither hypothesis) (Dienes, 2014).

Target-locked ERPs

To investigate if PA after-effects could manifest as a gain modulation of visual responses (post-stimulus attention effect), rather than in preparatory, pre-stimulus activity, we analysed ERPs locked to the visual target (also serving as motor cues) (only large targets included). For each participant and condition, EEG was low-pass filtered at 30Hz and then segmented in 600ms epochs, from 100ms before to 500ms after target presentation. All epochs were baseline corrected to 100ms pre-stimulus activity and averaged over blocks of recording in each condition (pre/post Prism, pre/post Neutral). P1- and N1-peaks were then extracted as the most prominent positive and negative peaks over parieto-occipital electrodes (PO7 and PO8) within the 70-150ms (P1) and 130-230ms (N1) intervals after target onset, and analysed for attentional and PA modulation, in line with previous studies (Eimer, 1994, Martín-Arévalo at al., 2016a).

Statistical analysis: For each component of interest (P1 and N1), changes in peak amplitude and latency were analysed through repeated measure ANOVAs testing the factors Exposure Type (Prism *vs.* Neutral), Time (Pre *vs.* Post), Cueing (Valid *vs.* Invalid), Target position (Left *vs.* Right) and Laterality (Contralateral *vs*. Ipsilateral to the target position).

Results

Prismatic adaptation: expected leftward bias after adaptation to rightward-shifting lenses

Analysis of pointing displacement during PA revealed the expected pattern (**Fig. 3**). When wearing rightward-shifting lenses (solid line), participants showed an initial rightward pointing deviation during early exposure (positive deflection) that was compensated for in the late exposure stage. This is explained by adaptation, given that post-exposure pointing was associated with an after-effect characterized by a leftward overshoot (negative deflection in Fig 3). No such effects were observed with neutral lenses (dashed line). This was statistically supported by a 2x5 repeated-measures ANOVA revealing significant main effects of Exposure Type [F(1,15) = 5.75, p = .03, $\eta p^2 = .28$] and Time [F(4,60) = 118.43, $p < .001$, $\eta p^2 = .89$] and a Exposure type x Time interaction [F(4,60) = 104.93, $p < .001$, $\eta p^2 = .87$]. Two repeated measures ANOVAs performed separately for each Exposure Type (Prismatic *vs*. Neutral lenses) both showed significant main effects of Time (Prismatic [F(4,60) = 173.45, $p < .001$, $\eta p^2 = .92$]; Neutral [F(4,60) = 17.01, $p < .001$, $\eta p^2 = .53$], each explained by different changes across PA stages. While wearing prisms, participants significantly pointed more rightward during the early exposure phase as compared to the pre-exposure (free-viewing) baseline ([F(1,15) = 74.72, $p < .001$, , $\eta p^2 = .83$], .04° *vs.* 2.38°). This bias disappeared during late exposure ([F(1,15) = .04, $p = .83$, $\eta p^2 = .00$], 2.38° *vs.* .07°). In the post-exposure phase, a significant leftward after-effect was observed in comparison to the pre-exposure blinded baseline ([F(1,15) = 121.35, $p < .001$, $\eta p^2 = .92$], -1.62° *vs.* -5.53°). In contrast, when wearing neutral lenses, participants showed a shift to the left in the early-exposure phase ([F(1,15) = 33.84, $p < .001$, $\eta p^2 = .69$], 0.0° *vs.* -.44°), but no significant after-effect post-exposure ([F(1,15) = .09, $p = .76$, $\eta p^2 = .00$] -1.46° *vs.* -1.36°).

Alternatively, comparing each PA stage between the two conditions revealed no significant difference in pointing performance during pre-exposure (both free-viewing and blinded) and late exposure (all *ps* > .43), whereas prismatic lenses induced a rightward shift during early exposure (Prism *vs*. Neutral: [F(1,15) = 116.77, $p < .001$, $\eta p^2 = .89$], 2.38° *vs.* -.44°) and a leftward after-effect (Prism *vs*. Neutral post-exposure: [F(1,15) = 158.09, $p < .001$, $\eta p^2 = .91$], -5.53° *vs.* -1.36°).

Behavioural data: Attentional and motor task performance

Hit rates to small targets/motor cues (indexed by correct responses to the delayed go-signals) were analysed to ensure participants did engage in attentional orienting using a repeated measure ANOVA with the factors Exposure type (Prism *vs.* Neutral), Time (Pre *vs.* Post exposure), Attentional Cueing (Valid *vs.* Invalid) and Target position (Left *vs*. Right). As expected, we found a significant main effect of Attentional Cueing [F(1,15) = 63.82, $p < .001$, $\eta p^2 = .81$] with more hits at validly cued than invalidly cued positions (0.83±0.03 *vs.* 0.63±0.02) indicating that participants were correctly shifting their attention to the cued location. We also found significant interactions of Time x Attentional Cueing [F(1,15) = 39.31, $p < .001$, $\eta p^2 = .72$], Exposure Type x Target position [F(1,15) = 4.96, $p = .04$, $\eta p^2 = .25$] and Attentional Cueing x Target position [F(1,15) = 4.83, $p = .04$, $\eta p^2 = .24$]. However, there was no effect in the main interactions of interest (Exposure type x Time x Attentional Cueing: $p > 0.35$) and no 4-way interaction with Target position ($p > .35$) suggesting that PA had not affected attentional processes at any target position.

Hit rates to large targets/motor cues and reaction times to go-signals were analysed to ensure that participants engaged well in motor preparation prior to the go signal (presented 1500ms after the motor preparation cue). This was supported by high accuracy approaching ceiling (left motor: 0.97±0.2, right motor: 0.96±0.3) and fast reaction times (left motor: 291±17.8ms, right: motor: 294±16.7ms). In addition, in only a small proportion of trials (4%) were participants slower than 500ms (the response deadline). Hence, participants were engaging in the motor preparation task. Statistical analysis using repeated-measures ANOVAs on both accuracy and reaction times to large targets, taking into account Exposure type (Prism *vs.* Neutral), Time (Pre *vs.* Post exposure), and

Hand (Left and Right) as factors, did not reveal any significant main effect nor interaction (all *ps* > .8).

PA after-effects on EEG signals

No evidence for PA to affect attention-modulated posterior alpha activity

The comparison between shifts of rightward versus leftward covert attention revealed the well-known alpha-signature of attention orienting. As illustrated by the time-frequency representations (**Fig. 4A**), alpha power exhibited a sustained, asymmetric modulation over left versus right occipito-parietal sites (P3/4, P5/6, P7/8, PO3/4, PO7/8 and O1/2) in accordance with the attention focus, starting 200ms after the attentional cue and lasting up to target onset. Note that the mirror-symmetric pattern (see map topographies in Fig. 4A) indicates a decrease in alpha-power contralateral to the attended position and/or an increases ipsilaterally (topographies in Fig. 4A reflect $Power_{\text{Attention right}}$ - $Power_{\text{Attention left}}$ subtraction maps). Importantly, this signature was observed regardless of exposure type and time (pre- and post-Prism, pre- and post-Neutral) (compare the four rows in Fig. 4A)

To test for potential differences of attention-modulated alpha activity across conditions (pre- and post- Prism and Neutral), we first run a cluster-based permutation test (in the 8-12 Hz frequency band of interest post-cue) taking into account all electrodes. The analysis revealed no significant cluster in the main effect of interest (Exposure type x Time interaction, see **Fig. 4B**, right middle map). Therefore, although the attention related alpha modulation seemed to be slightly accentuated post-prism as compared to pre-prism (Fig. 4B, see upper left map), this was not statistically different from pre- to post-changes in the neutral condition (Fig. 4B, lower left map). To further inform this null result, we calculated the Bayes factor (BF). This was determined separately for the left and right hemispheres considering the difference in alpha-power changes (Pre vs. Post) between PA and neutral condition over those occipito-parietal electrodes showing the strongest alpha-power changes when collapsed across all conditions. We obtained a BF of 0.2 for the left hemisphere and a BF of 0.34 for the right hemisphere, thus providing evidence for the absence of PA effect on attentional orienting as measured by alpha-power modulations.

In addition to the above cluster-based analysis approach, we run an independent, electrode of interest (EOI)-based analysis, which further substantiated the absence of a PA after-effect, i.e. of a differential effects of time (Pre *vs.* Post) on attention-related alpha modulation as a function of Exposure type (Prism *vs.* Neutral). We calculated an Attentional Modulation Index (i.e. AMI = $(Power_{\text{Contralateral}} - Power_{\text{Ipsilateral}})/[Common\ Denominator]$) over posterior sites (P3/4, P5/6, P7/8, PO3/4, PO7/8 and O1/O2) per hemisphere and condition (see **Fig. 4C).** Positive values indicate attention modulations in the expected direction, i.e. less alpha power in the contra- vs ipsilateral condition (both numerator and denominator negative). An ANOVA testing the factors Exposure type (Prism *vs.* Neutral), Time (Pre *vs.* Post) and Hemisphere (Left *vs.* Right) showed no significant main effects or interactions (all *ps* > .12), in line with the results of the cluster-based analysis. BFs were again calculated for each hemisphere and supported a lack of PA after-effect on attentional orienting (BF = 0.21 and 0.36 for the left and right hemisphere).

PA affects preparatory motor signals in the beta but not the alpha-band

Fig. 5 and **6** show time-frequency representations of the EEG activity recorded in the motor preparatory window as difference between right and left hand movement preparation. In line with previous research (e.g, Pfurtscheller and Lopes Da Silva, 1999), preparatory motor activity was associated with a distinct signature in the alpha (Fig. 5A) and beta bands (Fig. 6A). This consisted of a sustained, asymmetric modulation of alpha/beta-activity over rolandic areas of the two hemispheres (i.e. most consistently observed over C3/CP3, C4/CP4) in accordance with the to-be-moved hand starting 500ms after the motor preparation cue. The mirror symmetric pattern for both alpha and beta activity post-cue (see maps in Fig, 5A and 6A) indicates that activity in these frequency bands decreased contralateral and/or increased ipsilateral to the planned movement (as topographies in Fig. 5A and 6A illustrate $Power_{\text{Right Hand}}$ - $Power_{\text{Left Hand}}$ subtraction maps). In analogy to the attentional epoch, these data were first analysed by running cluster-based permutation tests, followed by EOI-based analysis to examine after-effects of PA on motor related oscillatory signatures in the frequency bands of interest (here 8-12 and 16-25Hz),.

For the cluster-based analysis in the alpha band (Fig 5B), we did not find any significant effect in the interaction of interest (i.e. Exposure type x Time, see middle right map in Fig. 5B). Following up on this null result by calculating BF separately for the left and right hemispheres as above (but now considering the difference in alpha changes between PA and neutral condition over central electrodes showing the strongest alpha-power changes across all conditions) revealed a BF of 0.2 for the left hemisphere and a BF of 1.03 for the right hemisphere, thus indicating that our data are insensitive in distinguishing null and alternative hypotheses for the right hemisphere. Additional, independent analysis of the lateralization indices of motor preparatory activity (MPI = ($\text{Power}_{\text{Contralateral Hand}}$ - $\text{Power}_{\text{Ipsilateral Hand}}$)/[Common Denominator]) in the alpha band per hemisphere (i.e. over electrode pairs C3/CP3 and C4/CP4; Fig. 5C) also did not reveal any effects of PA on these signatures of motor preparation. The corresponding ANOVA testing the factors Exposure type (Prism *vs.* Neutral), Time (pre *vs.* post) and Hemisphere (left *vs.* right) revealed no significant main effects or interactions (all *ps* > .14; Fig. 5C). Please note that as for the analysis of

AMI, positive values indicate that power over EOIs was modulated in expected directions (contralateral power decrease and ipsilateral power increase). Again, BF calculations pointed to a null effect over the left hemisphere (BF=0.26) and insensitive data for the right hemisphere (BF=0.89).

However, when considering the beta band (Fig. 6), the cluster based permutation tests showed a significant Exposure type x Time interaction for a cluster including right central electrodes (Fig. 6B, middle right map, black dots illustrate the significant interaction cluster on top of the difference map) ($p < .03$). To break down this interaction, we run two separate follow-up cluster-based permutation tests to compare effects of intervention, (i.e. time: Pre *vs*. Post) for Prismatic and Neutral lenses separately. The analysis revealed a significant increase of beta power after prismatic exposure over a predominantly right lateralized centro-parietal cluster ($p = .008$) (Fig. 6B, upper left map), whereas no clusters significantly differentiated pre and post Neutral measurements ($p = 1$) (Fig. 6B, lower left map). The additional, independent analyses of MPI were in line with the cluster-based result (Fig. 6C). The corresponding ANOVA showed a significant Exposure type x Time x Hemisphere interaction [F(1,15) = 4.53, p =.05, $\eta p^2 = .23$]. Breaking down the interaction revealed a significant Time x Hemisphere interaction for the prism condition [F(1,15) = 5.49, $p = .03$, $\eta p^2 = .40$], due to an increase in beta-power modulation over the right hemisphere post PA relative to pre PA [F(1,15 = 4.28, $p = .015$, $\eta p^2 = .33$], whereas no such effect emerged for the left hemisphere ($p > .29$). No main effects or interaction were found for the Neutral condition ($p > .48$; Fig. 6C). The increased MPI in the beta-band over the right hemisphere after PA indicates enhanced motor preparatory activity in the right hemisphere, in line with the direction of the behavioural PA after-effect (leftward compensatory shift).

No effects of PA on attentional-modulated visual evoked potentials

Finally, visual evoked potentials to targets/motor cues were analysed for modulation by attention and prism exposure using repeated-measures ANOVAs with the factors Exposure type (Prism *vs*. Neutral), Time (Pre *vs*. Post), Cueing (Valid *vs*. Invalid), Target position (Left *vs*. Right) and Laterality (Contralateral *vs*. Ipsilateral hemisphere to the target position). Separate ANOVAs were conducted on peak amplitude and latency of each component of interest (P1 and N1).

<u>P1.</u> In line with previous studies (Eimer, 1994; Martín-Arévalo et al., 2016a), the ANOVAs on P1 amplitude and latency revealed a main effect of Cueing. P1 peak amplitude was smaller in valid as compared to invalid trials (F(1,15) = 6.29, p = .02, $\eta p^2 = .28$; 3.02 *vs*. 3.43 μV), but peaked earlier in valid than invalid trials ([F(1,15) = 5.38, p = .03, $\eta p^2 = .30$]; 119.9 *vs*. 124.3 ms). Moreover, a significant Cueing x Laterality interaction emerged for P1-latency, indicating a shorter

latency over the hemisphere contralateral to the target position for the valid compared to invalid trials (Cueing x Laterality [F(1,15) = 134.76, p < .001, ηp^2 = .90]; 108.2 *vs*. 142.5 ms), and an opposite pattern for the hemisphere ipsilateral to the target position ([F(1,15) = 50.99, p < .001, ηp2 = .78]; 131.70 *vs*. 106.00 ms). No significant interactions with Exposure type x time was found either for amplitude or latency (all ps > .69; **Fig. 7**).

N1. A similar pattern of result was found for the N1 component. Its amplitude was smaller for validly cued than invalidly cued targets (main effect of Cueing: F(1,15) = 8.10, p = .01, ηp^2 = .35; -4.35 *vs*. -4.98 µV), but peaked earlier for valid as compared to invalid trials (main effect of Cueing [F(1,15) = 14.59, p = .001, ηp^2 = .49]; 194.1 *vs*. 202.5 ms). A significant Cueing x Laterality interaction pointed to smaller amplitudes for validly cued vs. invalidly cued targets within the ipsilateral hemisphere ([F(1,15) = 28.33, p < .001, ηp^2 = .65]; -3.86 *vs*. -5.28 µV). No other significant main effects or interaction were found either for amplitude or latency (all *ps* > .08, Fig. 7).

Discussion

We tested to what extent adaptation to rightward shifting prisms can induce after-effect on visuo-spatial attention orienting and/or motor preparation by examining their EEG-correlates before and after prism exposure in healthy participants, in comparison to exposure to neutral lenses. We found significant after-effects of PA to rightward shifting prisms on motor preparatory activity in the beta-band. Rightward PA (leading to a compensatory leftward pointing error) enhanced preparatory rolandic beta activity over the right but not the left hemisphere (hence contralateral to the PA-induced behavioural effect). However, we did not find any PA after-effects on visuo-spatial attention orienting as indexed either by attention-modulated occipito-parietal alpha-activity in anticipation of a lateralized target, by attention-modulated visual evoked potentials to this target or behavioural changes. Moreover, we employed two analysis approaches to test for PA after-effects on EEG-signatures of attention orienting (cluster- and EOI-based) both pointing independently to null results, and a follow-up Bayes factor analysis provided support for the null hypothesis in terms of effects on attention orienting. We therefore interpret our findings to show that rightward prisms modulate motor but not attentional processes.

Differential after-effects of PA on EEG-signatures of motor preparation and visuo-spatial orienting

Our finding of differential PA outcomes on EEG-correlates of attentional and motor processes is in line with several previous behavioural studies in healthy participants and right brain damaged patients reporting PA effects to be related more to motor than pure attentional/perceptual functions and only detectable when the behavioural task requires an overt motor response (Dijkerman, et al., 2003; Farné et al., 2002; Ferber and Murray, 2005; Fortis et al., 2011, Leigh et al., 2014; Striemer and Danckert, 2010b; Striemer et al., 2016; for a review see Striemer and Danckert, 2010a). For example, Striemer and Danckert (2010b) found neglect patients to show a PA after-effect only for straight-ahead pointing and manual line bisection (i.e. tasks requiring active motor responses), but not for its perceptual variant (i.e. the landmark task isolating visuo-spatial judgments from motor responses). However, it cannot be ruled out that PA affects both motor and attentional processes, and that differential after-effects reflect different time courses of recovery (e.g. de-adaptation) that could not be resolved here with our block design. In line with this view, Schintu et al. (2014) have shown that sensorimotor and visuospatial after-effects to a single PA session last up to 35 minutes, but that while the sensorimotor effects are stable, the visuospatial effects fluctuate over time. The nature of the difference between PA after-effects on motor and attentional functions should be investigated further in future work.

A PA after-effect at the motor level, as revealed here for the first time by means of EEG, is in accord with a growing number of TMS-studies showing PA-induced effects on motor cortex excitability (Magnani et al., 2014; Martín-Arévalo 2016b; Schintu et al., 2016). This effect could either represent a direct modulation of motor cortex activity or an indirect consequence due to PA interaction with the function of connected areas. The available neuroimaging data seem to point to the latter scenario, because consistently showing a sustained activation of the cerebellum and parietal cortex during PA (Chapman et al., 2010; Luauté et al., 2006). The cerebellum has an important role in movement control and preparation (Brunia, 1992), by exerting inhibitory influences on M1 via cerebello-thalamo-cortical circuits (Purzner et al., 2007). Notably, even though spectral EEG-signatures of the cerebellum have not been fully elucidated, frequencies in the range of 13-25Hz have been identified within the cerebellar cortex (Courtemanche et al., 2002; O'Connor et al., 2002; Pellerin and Lamarre 1997) and in primates, synchronization between cerebellum and motor cortex has been observed within this frequency range (Soteropoulos and Baker, 2006). It seems therefore conceivable that the involvement of the cerebellum during PA plays an important role in inducing a change in motor cortex activity. Likewise, an influence on motor areas through the modulation of connected parietal cortex is conceivable.

Our finding of unchanged occipito-parietal EEG-signatures of attentional orienting is not in support of parietal attention functions playing a pivotal role in PA after-effect, at least for the tested population and experimental conditions (healthy participants and rightward shifting prisms). In line with our findings, evidence for PA effects on attentional tasks in healthy participants has been so far inconclusive. While some studies have reported PA effects (Berberovic et al., 2003; Martín-Arévalo et al., 2016a; Striemer et al., 2006), others failed to find behavioural effects irrespective of the direction of prismatic displacement (Berberovic et al., 2004; Bultitude et al., 2013; Morris et al., 2004; Nijboer et al., 2010). On the other hand, PA to rightward shifting prisms has repeatedly been shown to ameliorate neglect symptoms as indexed by changes in a large variety of tasks (Nijboer et al., 2008; Oliveri et al., 2013; Pisella et al., 2006; Rode et al., 2010; Striemer and Danckert, 2007; Striemer and Danckert, 2010a; Vangkilde and Habekost, 2010). To account for such generalised effects, it has been postulated that rightward deviating prisms alleviate neglect symptoms by modulating spatial attention, possibly through a change in dorsal visual stream activity (Pisella et al., 2006, Striemer and Danckert al., 2010a). Our null result in healthy participants in terms of redirection of attention to the opposite (left) space after rightward prism exposure may be linked to baseline performance in this population. Healthy participants typically show an over-attention to left space at baseline (pseudoneglect), that is likely caused by right parietal dominance for spatial attention (Cavezian et al., 2012; Thiebaut de Schotten et al., 2011; Benwell et al., 2014). It is therefore conceivable that while neglect may be alleviated by rightward prisms, causing a reorienting toward the left, neglected visual field, the use of rightward prisms may not be able to further accentuate the physiologic leftward bias in healthy participants, due to ceiling. This would be in line with a recent ERP study by Martín-Arévalo et al. (2016a) reporting leftward but not rightward deviating prisms to affect attention-related processes in healthy participants (namely attentional allocation and disengagement) using a spatial cueing task and examining ERP-changes in cue-locked N1 and target-locked P1 amplitude. In addition, it may be argued that we did not find any modulation of oscillatory signatures of anticipatory attention because PA may act at the level of exogenous, rather than endogenous orienting of attention, as suggested by a recent fMRI study (Crottaz-Herbette et al., 2014; see Clarke at al., 2016 for a detailed model of rightward PA effects on ventral attention system). However, if so, we should have observed PA after-effect on visual evoked potentials to targets, in particular in regard to processes indexing reorienting of attention (visual evoked potentials to targets at uncued positions), which was not the case. Overall, our data therefore do not support an attentional origin of the after-effect of right PA in healthy participants.

Differential after-effects of PA on preparatory motor activity in the beta versus alpha bands

We found that rolandic beta activity was modulated by prism exposure, while central alpha/mu rhythms were unaffected. Despite alpha and beta activity being both considered electrophysiological markers of motor processes, they have been proposed to originate from different neural sources and subserve different functions (Cheyne, 2013; Crone et al., 1998;

Pfurtscheller and Lopes da Silva, 1999; Salmelin and Hari, 1994; Tan et al., 2013). Alpha activity is observed in a wider network including sensorimotor and parietal areas (Tzagarakis et al., 2015) and its synchronization is thought to index inhibition of task irrelevant areas (Jensen and Mazaheri, 2010; Vukelić et al., 2014). In contrast, the rolandic beta rhythm is generated in sensorimotor areas (Ritter et al., 2008; Tzagarakis et al., 2015) and has been suggested to be more strictly related to motor functions (Baker, 2007; Kilavik et al., 2013; Veniero et al., 2011). For example, during motor imagery, rolandic alpha-activity is relevant for globally inhibiting alternative motor programs (Brinkman et al., 2016), while rolandic beta-activity is related to task-relevant movement selection (Brinkman et al., 2014, 2016). Moreover, during the cue interval of a cued, delayed motor task, the degree of rolandic beta modulation has been shown to directly reflect the extent of motor preparation (Tzagarakis et al., 2015). Therefore, besides further supporting a differential, functional role of rolandic alpha and beta activity, our finding of a selective modulation of beta activity suggests PA interaction with motor function at the level of movement initiation.

Conclusion

Collectively, our results suggest that the after-effects of rightward prisms in healthy participants primarily occur at the level of voluntary motor preparation but not attentional deployment, by revealing PA to selectively affect its oscillatory signatures. Our design and results could be used to further study the origin of PA after-effects in healthy participants and neglect patients for informing intervention, e.g. in terms of promising target sites and protocols for adjunct neglect therapy through combining prisms with transcranial brain stimulation (Bracco et al., 2017, see also O'Shea et al., 2017).

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Figure captions

Fig. 1 Experimental setup and paradigm. A. Experimental time line. **B.** Experimental paradigm. Each trial started with a fixation cross, followed by an attentional cue (the bottom left or right section of the central rhombus turning green) instructing participants to covertly attend to the left or right lower visual field placeholder. After 1500ms, a second, motor preparation cue (big or small triangle) appeared in the left or right placeholder (80% at attended and 20% at unattended position) pointing either to the left or to the right (probability of 50%). The motor preparation cue indicated which response (left or right hand) the participants needed to prepare. After another 1500ms, a go-signal (green vertical line) instructed participants to perform the prepared action. EEG was analysed in terms of oscillatory alpha- and beta-activity in the two 1500ms post-cue intervals, covering anticipatory attention and preparatory motor processes to the left or right side of space respectively, as well as in terms of visual evoked potentials to the motor cue (also serving as visual target).

Fig. 2 Prismatic adaptation (PA) setup and time line. Participants point to targets on a curved, transparent panel. Pre-exposure (prismatic goggles off) involves pointing in free-viewing conditions (both pointing movements and targets visible) followed by occluded (blinded) pointing to visible targets. Participants were then asked to wear the googles (rightward orientation or neutral lenses) during free-viewing pointing (exposure, goggles on). Adaptation is then tested immediately after exposure with blinded pointing to targets (after-effect).

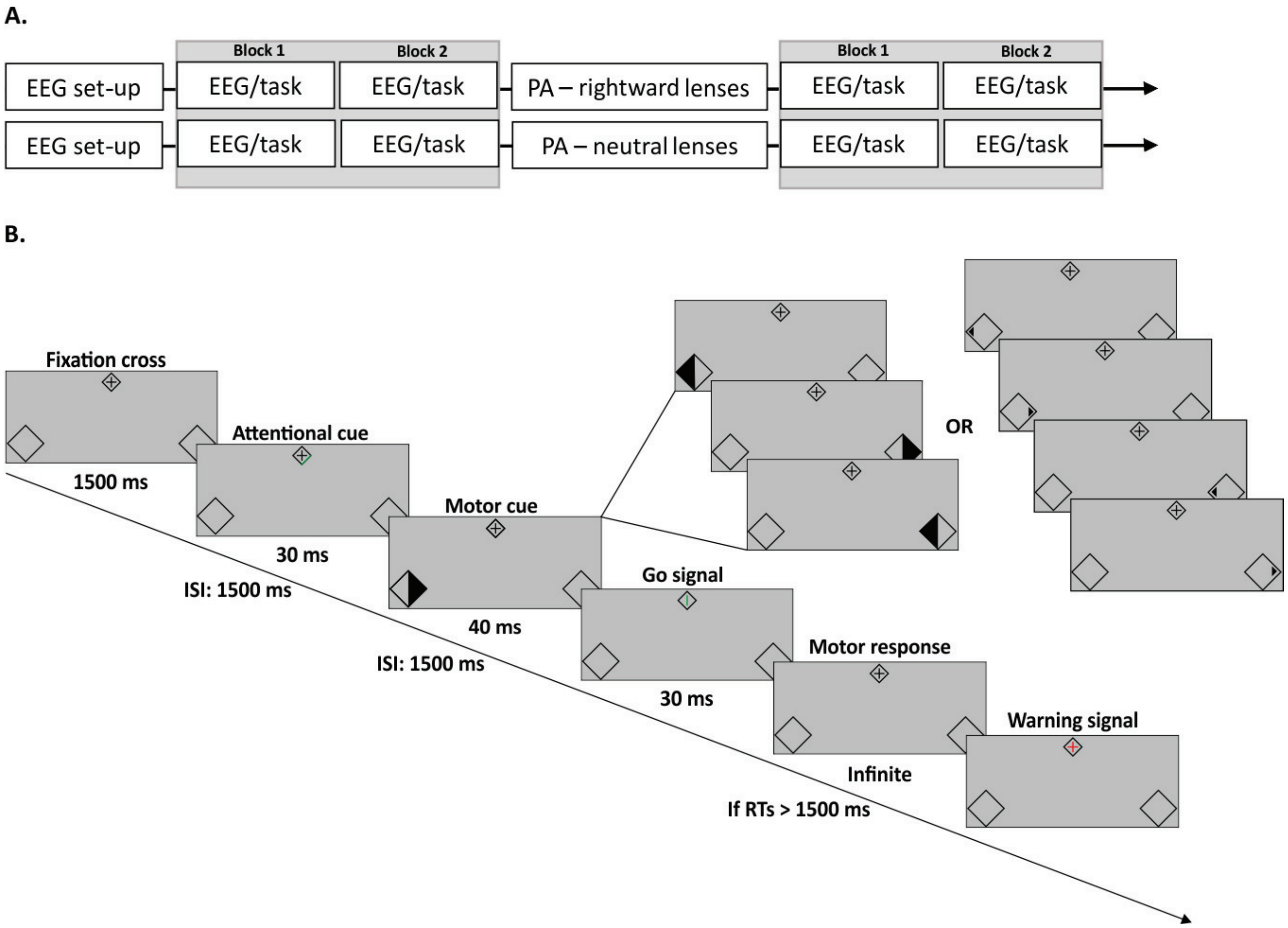
Fig. 3 PA pointing displacement. Mean pointing displacement (expressed in degrees of visual angle) throughout the prism adaptation procedure (pre-exposure free-viewing/pre-exposure blinded, early and late exposure, after-effect) are plotted for each condition. The solid line represents pointing when wearing real (prismatic) lenses (Prismatic goggles), whereas the dotted line represents pointing with neutral lenses (Neutral goggles). Negative values indicate a leftward pointing displacement; positive values a rightward displacement. Asterisks indicate a significant difference between conditions. Error bars represent sem,. $*p < .001$

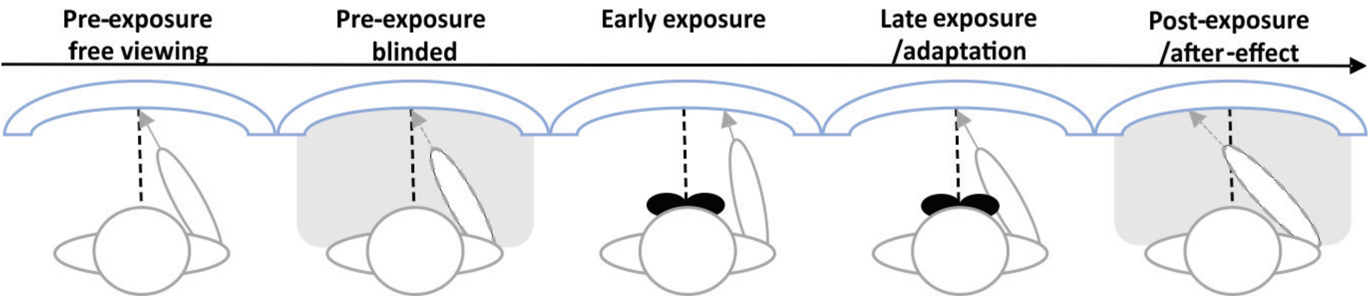
Fig. 4 Alpha modulation by attention orienting. A. Time-frequency representations (TFR) of the anticipatory attention related alpha modulation are shown separately across rows for each PA conditions (pre/post Prism, pre/post Neutral) for two posterior EOIs (left and right columns) by contrasting attention right and attention left trials [(Power$_{\text{Attention right}}$ - Power$_{\text{Attention left}}$)/common denominator]. The electrodes included in the left and right EOIs are indicated by black dots in the central maps (P3/4, P5/6, P7/8, PO3/4, PO7/8 and O1/2). The middle column represents the topography of alpha modulation (8-12Hz) between 0.2 and 1sec after attentional cue onset (black rectangle). **B.** Cluster-based analysis: Difference maps of alpha modulation between conditions (8-12Hz, 0.2-1sec post-cue). Raw effects are shown for each simple comparison on the left (pre-vs post-prism; pre-vs post-neutral) and for the Exposure x PA interaction on the right. No significant differences were identified by cluster based statistics (all *ps* > .05). C. EOIs analysis: Attentional modulation index [AMI = (Power$_{\text{Attention Contra}}$ - Power$_{\text{Attention Ipsi}}$)/ average over all conditions]) in the alpha band (8-12 Hz, 0.2-1sec) over posterior sites (P3/4, P5/6, P7/8, PO3/4, PO7/8, O1/2). Statistical analysis revealed no significant 2x2 interactions. Error bars: sem.

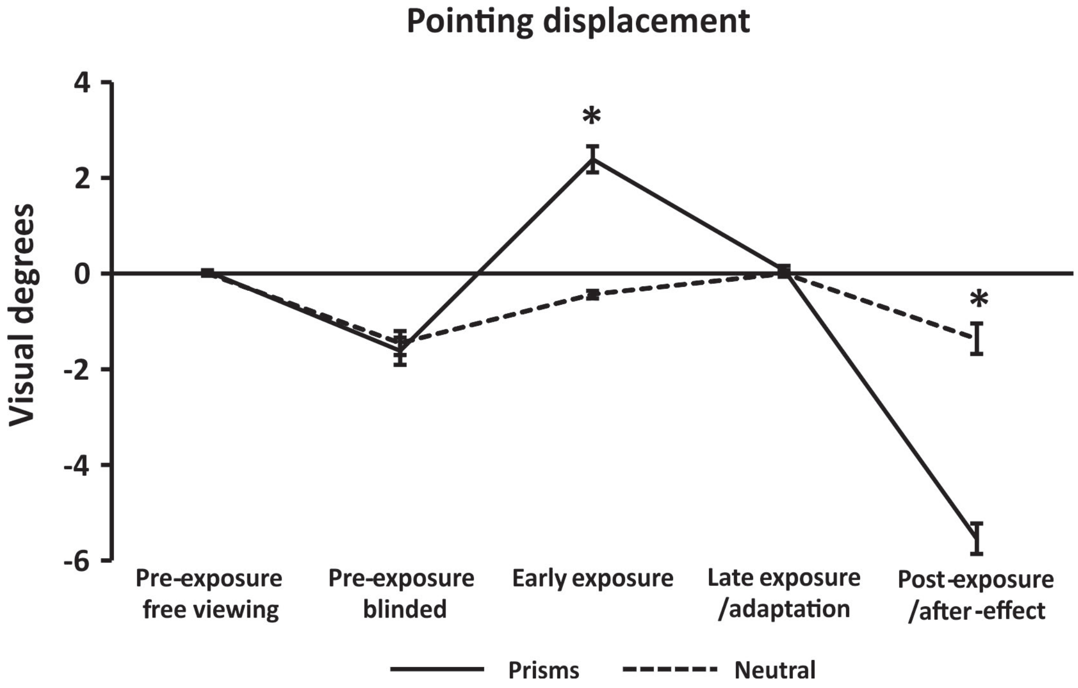
Fig. 5 Alpha/mu modulation by motor preparation. A. Time-frequency representations (TFR) of the motor preparation related alpha/mu modulation are shown separately across rows for each PA conditions (pre/post Prism, pre/post Neutral) for two central EOIs (left and right columns) by contrasting right and left hand motor preparation trials [(*Power*$_{\text{Right Hand}}$ - *Power*$_{\text{Left Hand}}$))/common denominator]. The electrodes included in the left and right EOIs are indicated by black dots (C3/4, CP3/4) in the central maps. The middle column represents the topography of alpha modulation (8-12 Hz) between 0.5 and 1.2sec after motor cue onset (black rectangle). **B.** Cluster-based analysis: Difference maps of alpha modulation between conditions (8-12Hz). Raw effects are shown for each simple comparison on the left (pre-vs post-Prism; pre-vs post-Neutral) and for the Exposure x PA interaction on the right. No significant cluster was identified (*p* > .05). **C.** EOIs analysis: Motor preparation index [MPI = (Power$_{\text{Hand Contra}}$ – Power$_{\text{Hand Ipsi}}$)/ average over all conditions] in the mu band (8-12 Hz, 0.5-1.2sec) over central sites (C3/4, CP3/4). Statistical analysis revealed no significant 2x2 interactions. Error bars: sem.

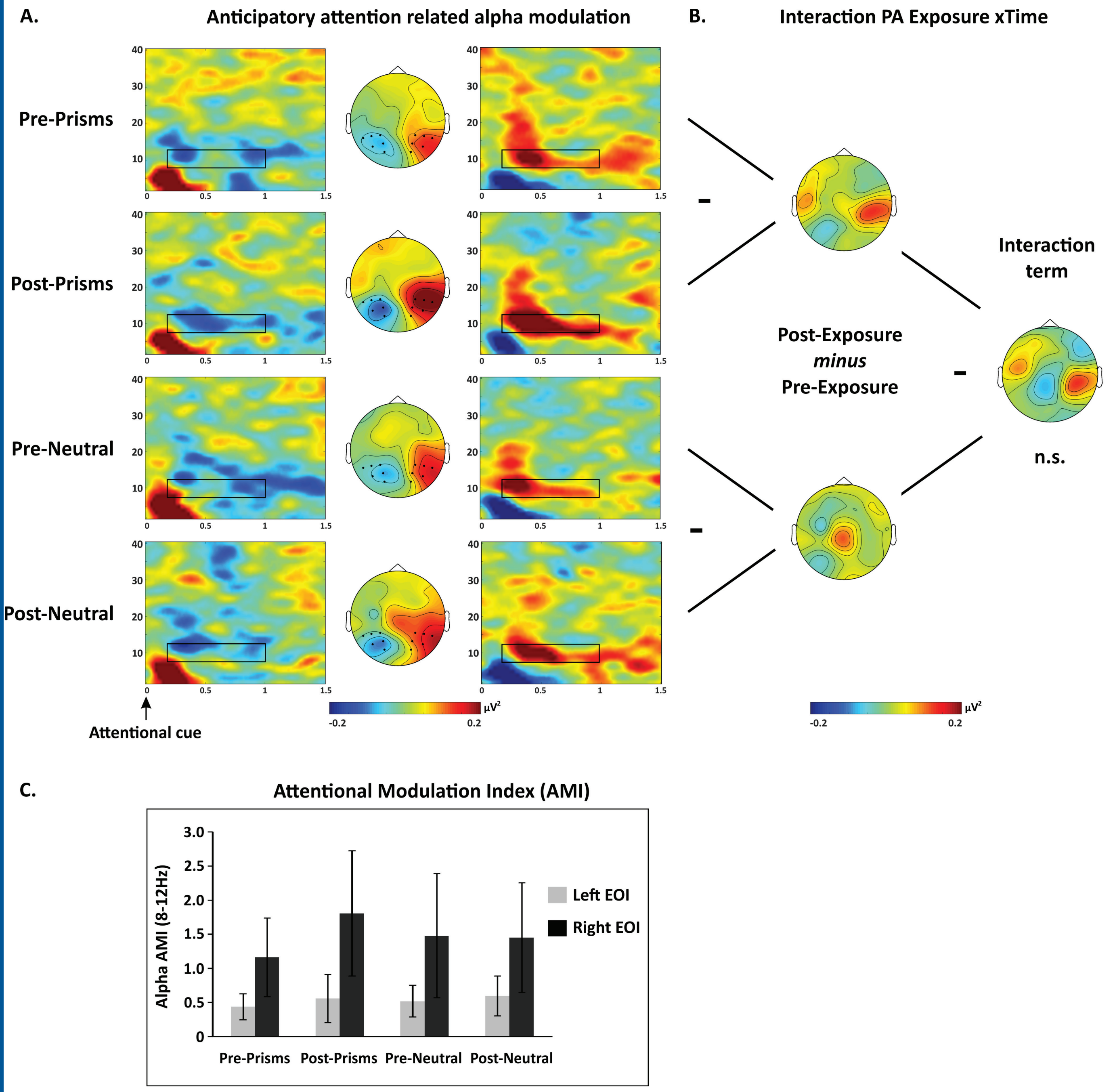
Fig. 6 Beta modulation by motor preparation. A. Time-frequency representations (TFR) of the motor preparation related beta modulation are shown separately across rows for each PA conditions (pre/post Prism, pre/post Neutral) for two central EOIs (left and right columns) by contrasting right and left hand motor preparation trials [(*Power*$_{\text{Right Hand}}$ - *Power*$_{\text{Left Hand}}$))/common denominator]. The electrodes included in the left and right EOIs are indicated by black dots (C3/4, CP3/4) in the central maps. The middle column represents the topography of beta modulations (16-25 Hz) between 0.5 and 1.2sec after the cue (black rectangle). **B.** Cluster-based analysis: Difference maps of beta modulation between conditions (16-25Hz, 0.5-1.2sec post motor cue). Raw effects are shown for each simple comparison on the left (pre-vs post-prism; pre-vs post-neutral) and for the Exposure x PA interaction on the right. 2x2 (Prism/Neutral vs. Pre/Post) cluster-based permutation analyses identified a significant interaction cluster ($p < .03$, see black dots in right interaction map). Follow-up simple tests revealed a significant cluster ($p = .008$) for Pre versus Post Prism PA but not for Pre versus Post neutral lenses (see left maps). **C.** EOIs analysis: Motor preparation index [MPI = (Power$_{\text{Hand Contra}}$ – Power$_{\text{Hand Ipsi}}$)/ average over all conditions] in the beta band (16-25Hz, 0.5-1.2sec) over central sites (C3/4, CP3/4). Note that positive values indicate the expected, contra- vs ipsi-lateral modulation. Statistical analysis revealed a significant interaction of Exposure x Time x Hemisphere ($p<.05$). The MPI over the right hemisphere increased post-PA ($p = .015$). Error bars: sem.

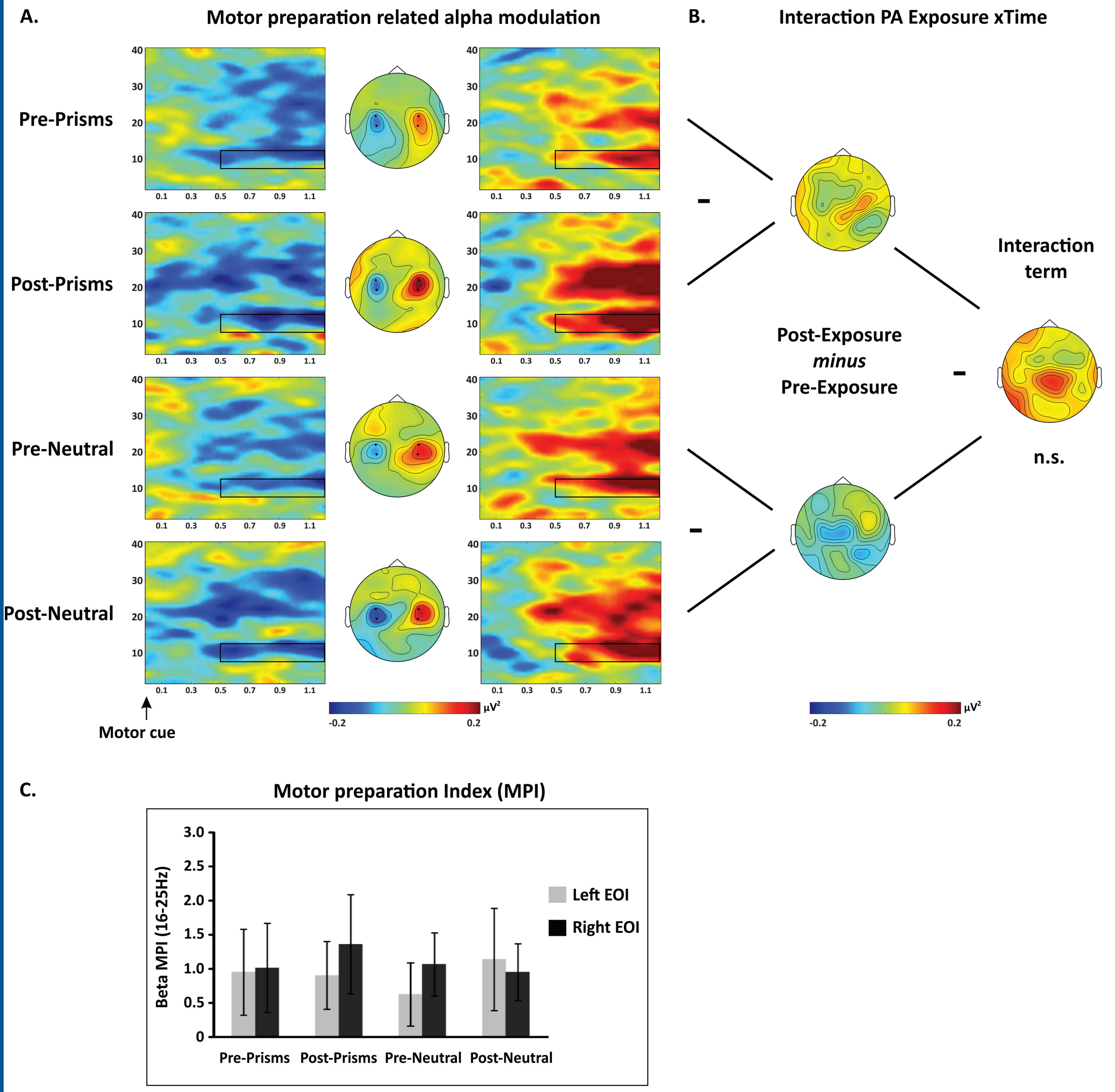
Fig. 7 Event-related potentials (ERPs) to targets/motor cues. A. P1 and **B.** N1 amplitudes and latencies before and after PA (Prism condition on the left and Neutral control on the right) are shown separately for hemispheres (ipsilateral and contralateral to the target position), validity of attentional cueing (valid and invalid), and target position (left and right). Anticipatory attention modulated the amplitude and latency of the P1 and N1-components independently of PA. Electrodes: PO7/8.

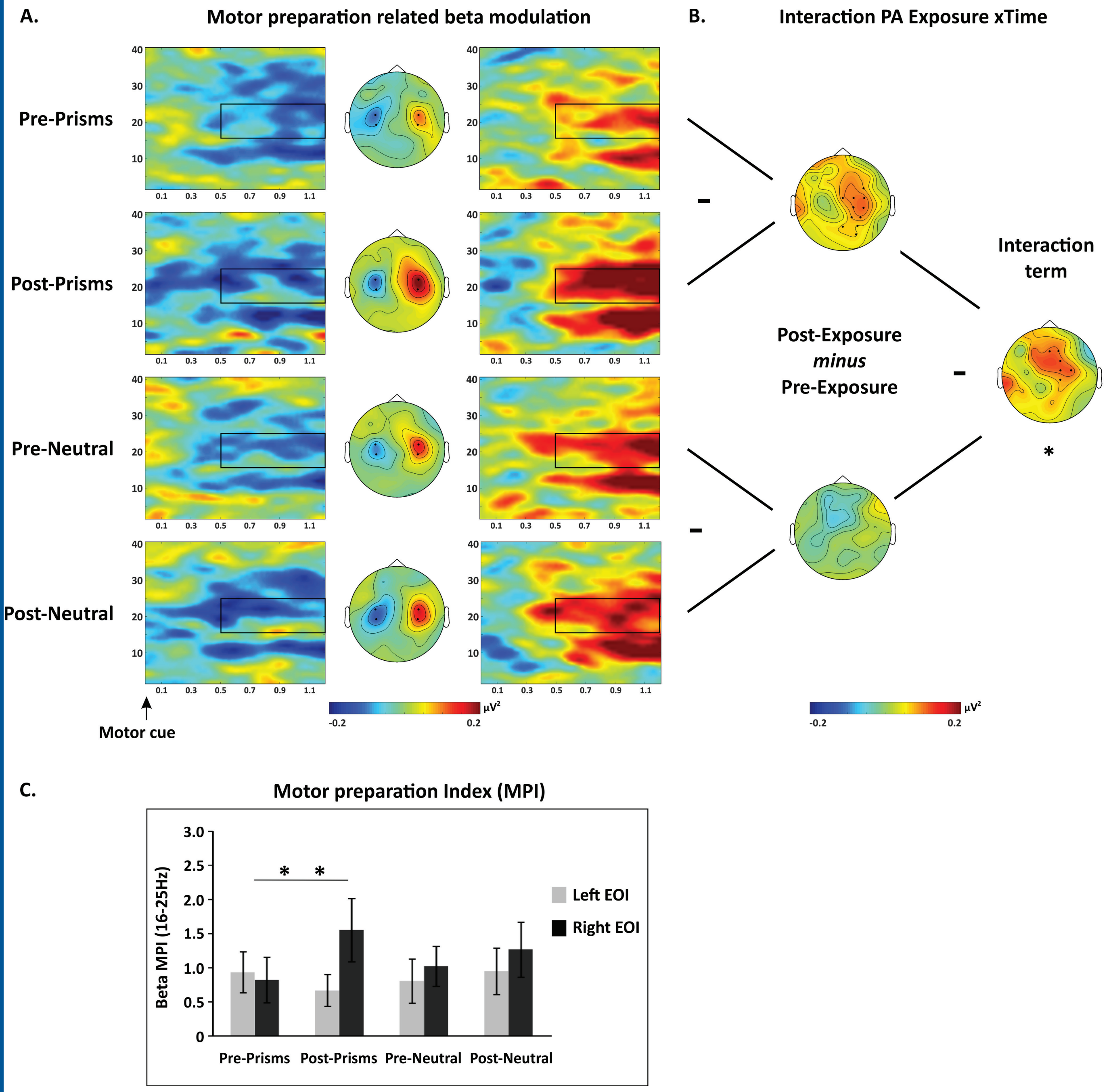

A.
Block 1
Block 2
EEG set-up
EEG/task
EEG/task
PA – rightward lenses
Block 1
Block 2
EEG/task
EEG/task
EEG set-up
EEG/task
EEG/task
PA – neutral lenses
EEG/task
EEG/task
B.
Fixation cross
1500 ms
Attentional cue
30 ms
ISI: 1500 ms
Motor cue
40 ms
ISI: 1500 ms
Go signal
30 ms
Motor response
Infinite
If RTs > 1500 ms
Warning signal
OR

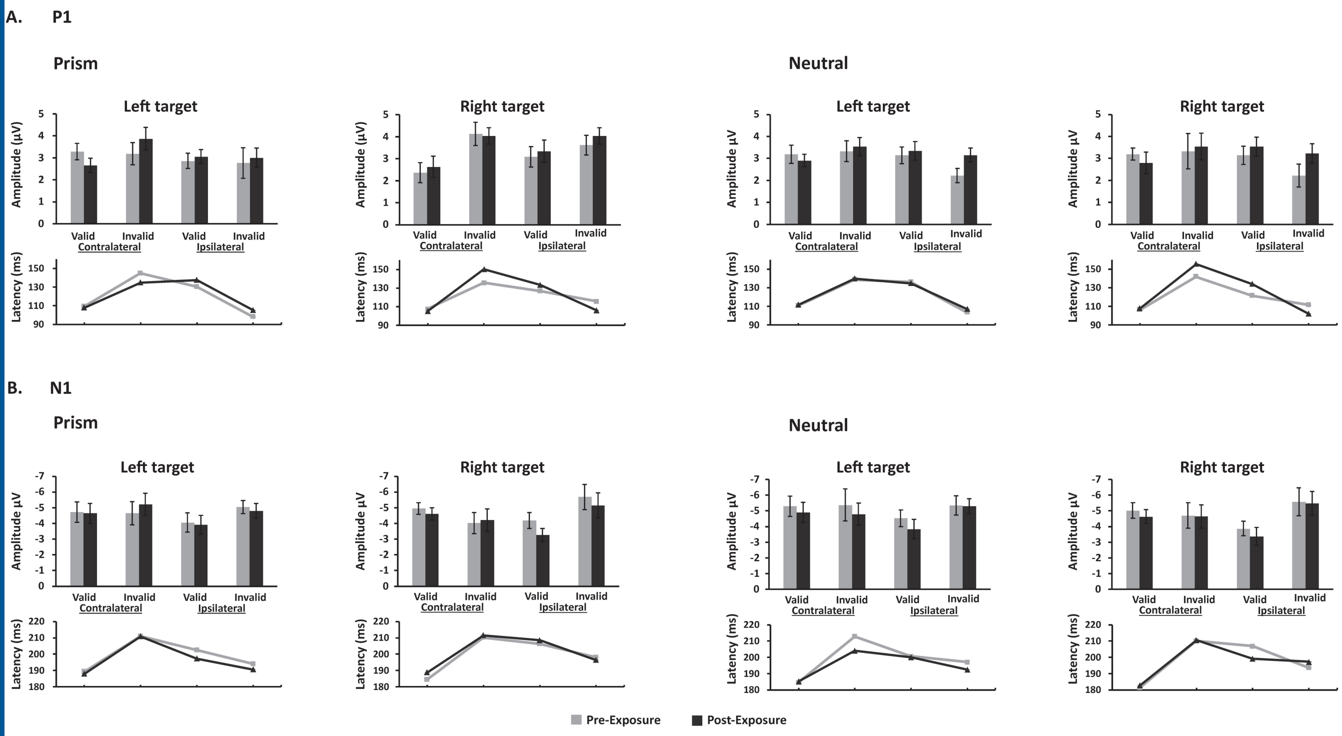

Pre-exposure
free viewing
Pre-exposure
blinded
Early exposure
Late exposure
/adaptation
Post-exposure
/after-effect


Pointing displacement
Visual degrees
4
2
0
-2
-4
-6
*
*
Pre-exposure free viewing
Pre-exposure blinded
Early exposure
Late exposure /adaptation
Post-exposure /after-effect
Prisms
Neutral


A.
Anticipatory attention related alpha modulation
B.
Interaction PA Exposure xTime
Pre-Prisms
Post-Prisms
Pre-Neutral
Post-Neutral
40
30
20
10
0
0.5
1
1.5
Attentional cue
-0.2
0.2
μV²
-
Post-Exposure
minus
Pre-Exposure
Interaction
term
n.s.
C.
Attentional Modulation Index (AMI)
Alpha AMI (8-12Hz)
3.0
2.5
2.0
1.5
1.0
0.5
0
Left EOI
Right EOI
Pre-Prisms
Post-Prisms
Pre-Neutral
Post-Neutral


A.
Motor preparation related alpha modulation
Pre-Prisms
Post-Prisms
Pre-Neutral
Post-Neutral
40
30
20
10
0.1
0.3
0.5
0.7
0.9
1.1
Motor cue
-0.2
0.2
μV²
B.
Interaction PA Exposure xTime
-
Post-Exposure
minus
Pre-Exposure
-
Interaction
term
-
n.s.
-0.2
0.2
μV²
C.
Motor preparation Index (MPI)
Beta MPI (16-25Hz)
3.0
2.5
2.0
1.5
1.0
0.5
0
Pre-Prisms
Post-Prisms
Pre-Neutral
Post-Neutral
Left EOI
Right EOI


A.
Motor preparation related beta modulation
Pre-Prisms
Post-Prisms
Pre-Neutral
Post-Neutral
40
30
20
10
0.1
0.3
0.5
0.7
0.9
1.1
Motor cue
-0.2
0.2
µV²
-
-
B.
Interaction PA Exposure xTime
Post-Exposure
minus
Pre-Exposure
Interaction
term
-
*
C.
Motor preparation Index (MPI)
Beta MPI (16-25Hz)
3.0
2.5
2.0
1.5
1.0
0.5
0
* *
Left EOI
Right EOI
Pre-Prisms
Post-Prisms
Pre-Neutral
Post-Neutral


A.
P1
Prism
Neutral
Left target
Right target
Amplitude (µV)
Amplitude µV
Latency (ms)
Valid
Invalid
Contralateral
Ipsilateral
B.
N1
Prism
Neutral
Left target
Right target
Amplitude µV
Latency (ms)
Pre-Exposure
Post-Exposure