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(Article begins on next page)

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Spatial Attention Modulation of the Brain Network Involved in Mental Time Travel

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Abstract

Objectives: the ability to Mental Time Travel (MTT) consists in moving along a cognitive and spatially oriented representation of time, i.e., an ideal Mental Time Line, where past and future events are respectively located on the left and on the right portion of such a line. A shift of spatial attention by prismatic adaptation (PA) influences this spatial coding of time, thus affecting MTT. Here, we investigated the neural correlates of such a spatial modulation on MTT in an fMRI protocol. ***Methods:*** to study MTT ability, participants were asked to indicate if a series of events took place before or after (Self-Reference component) an imagined self-location in time (Past, Present or Future; Self-Projection component), where they had to project themselves. The MTT task was performed before and after PA inducing a leftward shift of spatial attention, which is supposed to move towards the left portion of MTL, where Past is represented. ***Results:*** Following PA, we observed a facilitation in responding to past as compared to future events when participants projected themselves to the Past projection. As a functional counterpart of this behavioral finding, we propose a model of the brain activity modulations following the PA effects on MTT. ***Conclusions:*** as a result of the shift of spatial attention toward the left,

the facilitation in having access to past events is associated with the inhibition of superior frontal gyrus in the left hemisphere, whereas the facilitation in projecting towards the Past may result from the activity modulation in right and left inferior parietal lobule.

Keywords: Mental Time Travel, prismatic adaptation, time perception, spatial attention, functional MRI.

Key points

Question: In this study for the first time in literature we investigated the neural bases underpinning the effects of the deviation of spatial attention induced by prismatic adaptation (PA) while performing a Mental Time Travel (MTT) task. Finding: Our results showed that PA affects the activations of parietal and temporal areas bilaterally and of the left superior frontal gyrus. This network could mediate the behavioral improvement we found at the MTT task in healthy populations. Importance: We proposed a model of the functional modulation of the brain areas involved in attentional and temporal processing. Thus, it could be useful to understand and predict selective cognitive deficits following lesions in these brain areas. Next steps: Future research will focus on how the mechanisms underlying PA effects are modified and mediate the rehabilitation of spatial and temporal deficits in neglect patients.

Spatial attention modulation of the brain network involved in Mental Time Travel

We constantly re-evoke previous experiences and anticipate future possibilities to appropriately respond to stimuli in our environment. This ability is defined as Mental Time Travel (MTT), i.e., the human capacity to relocate themselves into another temporally specified location, both to the past and to the future (Dafni-Merom and Arzy, 2020; see also Addis et al., 2007; D'Argembeau, 2020; Garcia-Pelegrin et al., 2021; Schacter and Addis, 2007). It is widely accepted that moving to the past during MTT requires episodic autobiographical memory, that is, the ability to re-experience personal past events, whereas moving to the future requires "episodic future thinking", that is, the ability to project oneself forward to a potential future (Fellows and Farah, 2005; Buckner and Carroll, 2007; Gilbert and Wilson, 2007). The resulting capacity of reconstructing past events and anticipating possible scenarios also depends on semantic memory, as the envisioned events need to be consistent with the general knowledge of oneself and of the world (Suddendorf and Corballis, 2007).

In addition to these cognitive functions, it has been suggested that spatial representations shape time processing. According to this hypothesis, we represent temporal events on a spatially oriented line. Indeed, both temporal duration (short/long) and temporal concepts (before/after, past/future) can be represented along the Mental Time Line (MTL), a spatial continuum with a left-to-right spatial order, especially in western culture (Lakoff and Johnson, 1999; Oliveri et al., 2009; Bonato et al., 2012, 2016). Coherently with this hypothesis, MTT would consist in travelling along such a mental line, where past events are located on the left of future ones (Torralbo et al., 2006; Santiago et al., 2007; Arzy et al., 2008, 2009a, 2009b; Ouellet et al., 2010).

To better understand the mechanisms underlying MTT, Arzy and colleagues (2009b) implemented a functional Magnetic Resonance Imaging (fMRI) paradigm in which participants were asked to "project" themselves to past, present, or future moments in time (Self-Projection). Then, they were required to determine whether a given event had already happened (relative past) or had yet to

happen (relative future) with respect to the assumed specific Self-Projection in time (Self-Reference). Assuming a different time perspective, that is, projecting ourselves into the future or into the past, requires a cognitive effort that we pay in terms of accuracy and speed ("switching cost"): participants' performances get worse in Past and Future than in present Self Projection (Arzy et al., 2008; Anelli et al., 2016a, 2016b; Gauthier et al., 2019; Ciaramelli et al., 2021a). When projecting oneself in time, humans not only recall and predict events, but also change their mental perspective on life events. Thus, the same events can be located differently in the past or in the future: for example, the last five years events are future if we project ourselves back to ten years ago, or they are past events if seen from the present time.

Moreover, it has been proposed that the spatial time representation is accessed through spatial attention mechanisms (Bonato et al., 2012). In support of this hypothesis, the shift of visuo-spatial attention induced by the prismatic adaptation (PA) technique (Rossetti et al., 1998; Rode et al., 2001; Frassinetti et al., 2002; Pisella et al., 2006; Serino et al., 2007; Patané et al., 2016; Schintu et al., 2017) has been demonstrated to affect MTT (Anelli et al., 2016b). During the PA procedure, participants are asked to perform repetitive pointing movements toward a visual target while wearing a pair of goggles with prismatic lenses, which laterally deviate the visual field. Once the prismatic lenses are removed, a contralateral shift of the spatial attention is induced. Notably, Anelli and colleagues (2016b) revealed that after PA inducing a leftward (rightward) shift of spatial attention, participants' performance in the MTT task improved for past (future) events as compared to before PA.

From a neuropsychological perspective, the effects of PA on MTT were further confirmed in a recent study with neglect patients, who after right brain damage are unable to orient attention toward stimuli presented or represented on the left side (Anelli et al., 2018; for reviews about the effects of PA on neglect see also Redding and Wallace, 2006; Newport and Schenk, 2012; Rode et al., 2017; Anelli and Frassinetti, 2019; Panico et al., 2020). After a single session of PA inducing a leftward shift of spatial

attention, neglect patients improved in correctly locating events on the mental line (Anelli et al., 2018), suggesting that temporo-parietal areas mediate not only visuospatial but also MTT-related processes. Previous neuroimaging findings on healthy participants showed that a network involving similar areas is active during MTT: the Self-Projection conditions activate the right anteromedial temporal lobe and bilateral posterior parietal cortex, whereas the Self-Reference conditions activate the left inferior frontal cortex, and insular and occipito-temporal cortices bilaterally (Arzy et al., 2009b, see also Gauthier et al., 2016, 2019). Furthermore, the prefrontal cortex plays a special role in MTT, as it is specifically involved in processing both future Self-Projection and future Self-Reference, as suggested by neuropsychological studies (Ciaramelli et al., 2021a; Stendardi et al., 2021).

Since there is only behavioral evidence for the effect of spatial attention on MTT, a crucial point needs to be addressed: which functional network mediates the effects of spatial attention on our ability to mentally travel in time. To this aim, we presented healthy participants with a MTT task in a single event fMRI protocol, before and after a session of PA. We hypothesized that PA shifting attention toward the left would induce an advantage in accessing information regarding the past (Anelli et al., 2016b).

At the neural level, we expected a fronto-tempo-parietal network to be involved in MTT. As far as the effect of PA, we predicted a modulation of posterior parietal cortex and superior temporal lobe activity, as suggested by literature on the visuospatial effects of PA (Koch et al., 2008; Luauté et al., 2009; Magnani et al., 2014). Finally, since the frontal areas are involved in future processing, as suggested by studies on MTT in brain damaged patients (Ciaramelli et al., 2021a), a decrease of prefrontal activity is expected as a consequence of PA shifting attention toward the left.

Materials and Methods

Participants

Thirty-eight right-handed (Oldfield, 1971) healthy volunteers, recruited among university students (mean age 24.8, age 19-29; 23 females), took part in the fMRI study. To verify their eligibility to MRI examination, participants were submitted to a clinical history questionnaire, according to the University Hospital of Modena guidelines, in order to exclude the presence of ferro-magnetic clips, implants, electrodes or devices on the body, and claustrophobia. Other exclusion criteria were: history of neurologic or psychiatric disorders or brain trauma, alcohol or drugs abuse. The sample size was set by means of *a priori* power analysis on G*Power 3 with a repeated measure ANOVA model, (effect size $f=0.25$, $\alpha= 0.05$, and power= 0.85). The sample size is also adequate for fMRI analysis according to Friston's study (2012). One participant was excluded from the analysis because of large head movements during the scanning sessions. All participants gave their written informed consent to their participation. The study was approved by the local ethics committee (Comitato Etico dell'Area Vasta Emilia Nord - CE 134/2014/SPER/AOUMO) and was conducted in accordance with the ethical standards of the Declaration of Helsinki (World Medical Association Declaration of Helsinki, 2013).

Procedure

Participants underwent an adapted version of the MTT task (Casadio et al. under review; Anelli et al., 2016b), before and after a prismatic adaptation session (Session condition – Pre-PA vs Post-PA). The MTT task was arranged in a jittered single event fMRI protocol. The entire set of stimuli was presented before the experimental session, in order to avoid novelty effects and to let participants familiarize with the stimuli.

Two sessions of 72 trials each were presented. Each session was comprised of two MRI runs of 8 minutes each, thus a single session lasted 16 minutes. Taking into account the MRI preparation, the average length of the post PA session, from the last trial of PA to the end of the MTT task, was mean ± SEM 27 ± 0.5 minutes. This ensured that the entire post PA session was performed within the duration of the PA after effects (30 minutes, as assessed by previous studies; Magnani, et al. 2014; see also Terruzzi, et al. 2021). Each trial started with a warning cue, a blue screen lasting 500 ms, then participants were asked to imagine themselves either in the Present or in the Past or in the Future - Self-Projection condition – according to the instructions (either “today” or “ten years ago” or “in ten years”), shown on the screen for the entire duration of the trial and pseudo-randomly alternated at each trial (Fig. 1). Then, participants listened to a brief auditory cue (2000 ms), recorded with the same female voice and presented through fMRI compatible headphones, describing either a personal (e.g. thirtieth birthday) or a non-personal event (e.g. Milan Expo). Events were chosen and adapted, because of the passing of time, from a validated list used in previous work (Anelli et al., 2016a, 2016b; Supplementary Table S1 in the Supplementary materials). Finally, the participants had to classify the event as past or future - Self-Reference condition - relatively to the adopted temporal self-location, responding as quickly and precisely as possible at the end of each auditory cue, using their index or medium fingers on a two-buttons keypad. To prevent the confounding effects of a possible motor facilitation due to the spatial representation of time, half of the participants used the index finger to respond “past” and the middle for “future”, the other half used the opposite association. Before the experimental task, participants performed a brief practice session of six trials. The inter-stimulus intervals were pseudo-randomised (range 0.5–19.7s) using the make_random_timing.py script from the AFNI package (https://afni.nimh.nih.gov/). Immediately after the PA procedure outside the scanner, participants performed the same fMRI MTT protocol. At the beginning and at the end of each run, a fixation condition (20s) was introduced, to record a baseline for the fMRI signal. Custom-made software

developed in our laboratory (http://digilander.libero.it/marco_serafini/stimoli_video/) was used for stimuli presentation and behavioral data collection. The same software was used to present the visual warning cue and the instructions via the ESys System remote display.

At the end of the experiment, participants completed a questionnaire evaluating their knowledge of the events by asking them to recollect when a given event happened in the past, or to estimate when a given event is likely to happen in the future. We used this questionnaire to categorize the trial responses of the MTT task for each participant as a function of his/her experience (e.g. in the Present Self-Projection, the "graduation" event stimulus was past for some of the participants, but future for others).

Prismatic adaptation procedure inducing leftward shift of spatial attention

Prismatic adaptation was performed outside the MRI scanner in an adjacent, quiet and separate room, following the same procedure of previous studies investigating the effects of PA on time perception (Magnani et al., 2013, 2014; Anelli et al., 2016b). It consisted in a pointing task towards a visual stimulus (a pen) in three experimental conditions: pre-exposure to prismatic lenses, exposure and post-exposure. The prismatic goggles induced a 10° rightward deviation of the visual field, and the visual stimuli were presented either straight in front of the participants (0°, center), or 21° to the left or to the right of the center. Participants had to point at the target with their right index finger, from a starting point on their chest, as fast and precisely as possible. The pre-exposure condition was comprised of 60 trials, half of them were in a closed loop (visible pointing, 30 trials) pointing condition, as the participants could see the trajectory of their movement, and half were in open loop (invisible pointing, 30 trials). In the exposure condition, participants had to point at the target while wearing the prismatic lenses in closed loop condition (90 trials). Finally, in the post-exposure condition participants removed

the goggles and performed the task again in an open loop condition (30 trials). The experimenter recorded the end position of the subject's pointing direction.

Control Experiment

Since participants underwent the MTT task twice in the fMRI Experiment, the behavioral improvement found after PA could be due to spurious effects, such as familiarization or task repetition. To rule out this possibility, we conducted a behavioural control experiment on a novel group of participants performing the MTT task, before and after a sham condition.

Thirty-seven right-handed (Oldfield, 1971) healthy volunteers, comparable with our previous sample for age, gender and educational level (mean age 22.9, range 19-27, 22 females), took part in the Control Experiment, after giving their written informed consent. The procedure was identical to the one adopted in the fMRI Experiment, except for the PA exposure, where a pair of goggles with neutral lenses was used. Since these lenses do not induce any deviation of the visual field, they do not affect spatial attention. Furthermore, the Control Experiment was conducted exclusively at the behavioral level as participants did not undergo MRI scanning during the MTT task.

MRI data collection

MRI data were collected on a 3T GE Signa Architect system over two experimental sessions (Pre-PA; Post-PA). Each session was comprised of two runs of 320 volumes and each run lasted 8 minutes, for a total of 16 minutes per session; each functional volume had 46 3mm-thick slices (TR= 1500ms, TE=30ms, voxel size 3x3x3mm). A high-resolution T1-weighted 3D anatomical image (TR= 2184.9ms, TE= 3ms, 46 slices, 1x1x1mm) was recorded for each participant to allow anatomical localization.

Data analysis

Since behavioral and beta values obtained from selected regions of interest (ROIs) of functional data were normally distributed in all conditions (all $p>0.05$ at Shapiro-Wilk test), ANOVAs were run and effect size was indicated as partial eta squared (η^2_p). When the interactions were significant, Duncan post-hoc tests were conducted. Mean values and standard error means (SEM) were reported for each condition.

Behavioral data

In order to obtain a combined, synthetic, and synoptic index, which provides precise information about the performance, the inverse efficiency score (IES) was calculated as the ratio between mean reaction time (RT) and proportion of correct answers: the higher the IES, the worse the performance.

To assess the participants' MTT ability, a repeated measures ANOVA, with Self-Projection (Past, Present, Future) and Self-Reference (past, future) as within-subject factors, was conducted on the IES obtained in the Pre-PA session. To evaluate the effect of PA, we conducted a similar ANOVA on Δ IES, the difference between the Pre-PA and Post-PA session: the higher Δ IES, the better the performance in the Post-PA as compared to the Pre-PA session.

Functional data

Functional data were pre-processed and analyzed using MatLab (Mathworks, Inc) and SPM12 (Wellcome Department of Imaging Neuroscience). The following pre-processing steps were used: slice-time, spatial realignment, normalization to MNI template and smoothing with 6mm full width Gaussian filter. Single-subject statistical analysis was performed applying the General Linear Model (GLM), where the time-series data were modeled as a series of events convolved with a canonical hemodynamic response function. Regressors of interest were as many as the combinations of factors, i.e., the

experimental conditions. Motor answer, errors and head-motion parameters (translations and rotations) were entered as nuisance variables.

Each experimental condition was compared to the baseline and the other conditions and individual contrast images were used for the whole brain random effect analysis.

Whole brain analysis. A full-factorial ANOVA with Session (Pre-PA, Post-PA), Self-Projection (Past, Present, Future) and Self-Reference (past, future) as factors was conducted on single-subject contrast images. In order to investigate the effects of PA on MTT ability, the following contrasts were considered: Pre-PA>Post-PA; Post- PA>Pre-PA (Magnani et al. 2014).

A double statistical threshold (voxel-wise $p<0.001$ and spatial extent) was applied to obtain a combined significance, corrected for multiple comparisons, of $\alpha>0.05$, as computed by 3dClustSim AFNI routine, using the "-acf" option. A family-wise error (FWE) correction was applied to the contrast Pre-PA>Post-PA.

Regions of interest (ROI) analysis. We evaluated cortical activations in both the Pre-PA and Post-PA sessions in several regions of interest (ROIs, each as an 8 mm radius sphere), extracting betas values with Marsbar (Brett et al., 2002). According to the literature, we selected:

- bilateral inferior parietal lobule (IPL, right x= 36, y= -52, z= 59; left x= -42, y= -70, z= 41; extracted from the Pre-PA vs Post-PA contrast); involved in mediating PA effects, spatial attention and spatial representation of time (Pisella et al., 2006; Arzy et al., 2009b; Crottaz-Herbette et al., 2014; Gauthier and van Wassenhove, 2016; Wilf et al., 2019; Panico et al., 2020);
- left superior frontal gyrus (SFG; x= -3, y= 56, z= 20; extracted from the Pre-PA vs Post-PA contrast), involved in time modulation mechanisms as a consequence of PA (Magnani et al., 2014);

- bilateral superior temporal gyrus (STG; right x= 45, y= -22, z= 5; left x= -45, y= -19, z= 2; extracted from the Post-PA vs Pre-PA contrast), involved in prismatic adaptation mechanisms and spatial attention (Karnath et al., 2001; Luauté et al., 2009; Panico et al., 2020).

Repeated measures ANOVAs were conducted on the beta values of the ROIs with Self-Projection (Past, Present, Future) and Self-Reference (past, future) as within-subjects factors, separately for Pre-PA session and Post-PA session. The same ANOVA was performed including factor Session to compare the Pre-PA and Post-PA. All the coordinates are in the MNI space atlas.

Pearson's correlation analyses were conducted between behavioral data (IES) and beta values.

Psycho-physiological interactions (PPI) analysis. The PPI analysis identifies brain regions whose activity depends on an interaction between psychological context (the experimental conditions) and physiological state (the time course of brain activity) of the seed region. Since recent findings suggest an involvement of IPL in PA, spatial attention and spatial representation of time (Pisella et al., 2006; Arzy et al., 2009b; Crottaz-Herbette et al., 2014; Gauthier and van Wassenhove, 2016; Wilf et al., 2019; Panico et al., 2020) we used right and left IPL as seeds. For each participant, the signal from the peak voxel in IPLs was extracted from the contrast past-events Past-projection>baseline. A 6-mm radius sphere was built around the activity peak to define a volume of interest (VOI; MNI average coordinates: right IPL: x=36.5, y= -52.1, z=51.4; left IPL: x= -36.9, y=-61.3, z=44.3). Each participant's data were re-modelled with regressors for: the time-course in the seed region (physiological regressor); the experimental condition (past-events Past-Projection>baseline; psychological regressor); the interaction between the experimental condition and the region of interest activation signal (psychophysiological interaction). The latter was chosen as the regressor of interest and the corresponding contrast images of the single-subject PPI analyses were used for the random-effect analysis (one-sample t-test).

Transparency and Openness

We report how we determined our sample size, all data exclusions, all manipulations, and all measures in the study. All data and research materials will be made available by the authors, without undue reservation. Data were analyzed using TIBCO Statistica™ software, version 14.0.1, and Jasp software, version 0.17.1. This study's design and its analysis were not pre-registered.

Results

We checked for possible differences between females and males both in the behavioural and in the functional data: since we found no significant difference, we analyzed the data from all the participants together.

Behavioral results

Pre-PA session

Analysis on IES revealed a significant main effect of Self-Projection ($F_{2,72}$=72.72, p<0.001, η^2_p=0.67), with all the conditions significantly different from each other (mean value Past = 4491 ± 109, Present = 3684 ± 71, Future = 3907 ± 73). The interaction Self-Projection*Self-Reference was significant ($F_{2,72}$=8.51, p<0.001, η^2_p=0.19; Supplementary Fig. S1). Post-hoc tests showed that performances for past events were significantly better as compared to future events when participants were projected to the Past (mean 4294 ± 137 vs 4688 ± 122, p<0.001). Furthermore, when participants were projected to the Future, a significantly better performance was found for future as compared to past events (mean 3784 ± 76 vs 4031 ± 107, p=0.04). In the Present projection, performance was comparable for past and future events (mean 3562 ± 82 vs 3806 ± 101, p=0.05).

Pre-PA minus Post-PA sessions: effect of prismatic adaptation on the MTT task

Analysis on Δ IES revealed a significant interaction of Self-Projection*Self-Reference ($F_{2,72}$=4.06, p=0.02, η^2_p=0.10). Post-hoc tests showed that performance for past events was significantly better than those for future events when participants were projected to the Past (mean 700 ± 99 vs 355 ± 134, p=0.02), and for past events when participants were in the Present projection (375 ± 58, p=0.03) (Fig. 2). Thus, the interaction revealed an improvement in performance in the Post-PA session for past as compared to future events when projected in the Past.

The main effects of Self-Projection (p=0.2) and Self-Reference (p=0.7) were not significant.

Prismatic adaptation (PA) effect

To verify the effect of PA (the error reduction of the initial pointing deviation in the exposure phase), a series of linear mixed effects models were conducted using the software Jasp (version 0.17.1) on the mean pointing deviation from the target, expressed in angle degrees, and the participants' random intercept; the trial number (1-30) was added in the model as fixed ordinal variable. To test whether the inclusion of the fixed independent variable trial number increased the model's goodness of fit, likelihood ratio tests (LRT) were conducted. A by-subject random intercept was also added to account for inter-subject variability in the adaptation procedure (Albini, et al., 2022). In the final model on the PA procedure, taking the trial number as fixed effect, we found a significant effect of the trial number ($\chi^2_{(29)}$ = 1300.87, p<0.001), with decreasing deviations from the target, along the PA (see Supplementary Fig. S2).

In order to verify the after-effect of PA, we compared the participants' displacement in the open loop (invisible) pointing in the Post-PA (last 30 trials) and Pre-PA conditions (half of the 60 trials in pre-exposure condition). A paired-samples t-test (two tailed) was conducted to compare the two conditions. A significant (t(36)=24.22; p<0.001) leftward deviation in the post-exposure was found as compared to

the pre-exposure condition (-6.1° ± 0.2 vs -0.5° ± 0.1; Supplementary Fig. S3), as evidence of the PA procedure efficacy.

Control experiment

The ANOVA on Δ IES (Pre-PA minus Post-PA sessions) did not reveal any significant main effect of factors (Self-Projection p=0.2; Self-Reference p=0.4) nor interaction (p=0.7). These results suggested that a repetition or familiarization with the task *per se* could not explain the effects found in the fMRI experiment.

Functional results

Whole brain analysis: Pre-PA>Post-PA

In the Pre-PA as compared to Post-PA session, a widespread network was activated involving, among others, right parahippocampal gyrus and postcentral gyrus, and bilateral posterior parietal Cortex (the IPLs, angular and supramarginal gyri), precuneus, occipital cortex, cerebellum, basal ganglia, inferior, middle and superior frontal gyri (Fig. 3A; Supplementary Table S2).

ROI analyses in Pre-PA session

Right IPL showed a significant main effect of Self-Projection ($F_{2,72}$=4.09; p=0.02, η^2_p=0.11), with a higher activation for the Future as compared to the Present projection (Fig. 3B). Interestingly, the beta values negatively correlated with IES in the Future projection (r=-0.3, p=0.03), indicating that the higher the right IPL activation, the lower the IES, i.e. the better the performance.

Left STG showed a significant main effect of Self-Reference ($F_{1,36}$=7.45, p<0.01, η^2_p=0.17) with a higher activation for past as compared to future events.

Finally, analysis on **left SFG** revealed a significant main effect of Self-Reference ($F_{1,36}$=7.59, $p<0.01$, η^2_p=0.17) with a positive activation for future events and a signal decrease for past ones (Fig. 3B).

Right STG and **left IPL** did not show any significant main effect ($p>0.1$ and $p>0.2$, respectively).

These results on the MTT task related activity (before PA) indicate that right IPL is more activated when participants were imagining themselves in the Future, whereas left STG and left SFG are involved in the Self-Reference component of MTT when participants responded to past and to future events, respectively.

Whole brain analysis: Post-PA>Pre-PA contrast

The analysis showed bilateral activation in STG underlies the PA effect (Fig. 4A; Table 1).

ROI analyses in Post-PA session

Right IPL did not show any significant main effect (all ps >0.07), indicating that this area was engaged during the MTT task, regardless of any experimental condition. However, beta values of right IPL negatively correlated with the participants' performance (IES) for future events when they were projected to the Past ($r=-0.3$, $p=0.05$): the lower the right IPL activation, the worse the performance.

In the **left** hemisphere, **IPL** showed a significant main effect of Self-Projection ($F_{2,72}$=5.39; $p<0.01$, η^2_p=0.13) with a positive and higher activation in Past projection as compared to Present and Future projections (Fig. 4B).

Moreover, analysis on **left SFG** showed significant main effects of Self-Projection ($F_{2,72}$=4.93, $p<0.01$, η^2_p=0.12), with a greater reduction of activation for Past as compared to Future projection, and of *Self-Reference* ($F_{1,36}$=7.77, $p<0.01$, η^2_p=0.18), showing negative beta values for both past and future events, with a greater reduction for past as compared to future events (Fig. 4B). The Self-

Projection*Self-Reference interaction ($F_{2,72}$=4.63, p=0.01, η^2_p=0.11) was also significant. Post-hoc analysis revealed a lower activation for past than for future events, when participants were projected both in the Future and in the Present (both p<0.05). Moreover, SFG displayed a significantly lower activation for future events in the Past projection as compared to future events in the Present and Future projections (both p<0.01).

The analysis on temporal regions in Post-PA indicated a significant main effects of Self-Projection ($F_{2,72}$=3.67, p<0.05, η^2_p=0.09) in **left STG**, with a higher activation in the Present as compared to Future projection, as well as a significant main effect of Self-Reference ($F_{1,36}$ =5.87, p=0.02, η^2_p=0.14) with a higher activation for past as compared to future events (Fig. 4B). On the contrary, in the right hemisphere, **right STG** did not show any significant effect (p>0.05).

Overall, these results showed that during Post-PA the right IPL is generally involved in the MTT task, the left IPL is more activated when participants projected to the Past, while the left SFG was less activated for future events.

ROI analyses with Session (Pre-PA, Post-PA) as factor

A significant main effect of *Session* was found in **right IPL** ($F_{1,36}$=25.68, p<0.001, η^2_p=0.42) and **left IPL** ($F_{1,36}$=28.69; p<0.001, η^2_p=0.44) in the ANOVAs conducted with Session (Pre-PA, Post-PA), Self-Projection (Past, Present, Future) and Self-Reference (past, future) as within-subjects factors. Both these areas showed a reduced activation in the Post-PA session (Fig. 5). Results from the analyses of the rest of the ROIs are reported Supplementary materials.

PPI analyses

Considering that the effect of PA at behavioral level was limited to past events in Past projection, we conducted PPI analyses evaluating the interaction of this condition with the BOLD signal in the right and left IPL.

Right IPL Post-PA did not show any significant positive correlation, whereas the connectivity decreased bilaterally with superior and middle temporal gyri, occipital cortices, insula, inferior and middle frontal gyri and parietal cortices, comprising superior parietal lobule, angular gyrus and precuneus (Supplementary Table S3).

Left IPL Post-PA showed a significant positive correlation with left superior frontal gyrus (Supplementary Table S4), whereas the connectivity decreased bilaterally with superior and middle temporal gyri, occipital cortices, inferior and middle frontal gyri and right inferior and superior parietal lobules, comprising precuneus and angular gyrus, and supplementary motor area (Supplementary Table S5; see also Fig. S3).

Discussion

In a single event fMRI protocol, we studied the neural activations during a MTT task before and after a single session of PA inducing a leftward shift of spatial attention. As a consequence of the manipulation of spatial attention, when participants were projected to the Past, the performance for past events improved, and concurrently a modulation of brain activity in the fronto-temporo-parietal network involved in the MTT task was observed. Specifically, bilateral IPL and left SFG reduced their activation, while bilateral STG increased its activation.

Consistent with behavioral studies, performance before PA worsened when participants were projected to a time location different from the Present. When participants are asked to imagine themselves in a specific time location (Past, Present or Future), they adopt a first person (egocentric) perspective. Once a given temporal location has been adopted, moving to a different location is

achieved by paying a switching cost in re-mapping their location on the MTL. Hence, this results in a cost on the MTT performance in terms of accuracy and speed (Arzy et al., 2009b; Anelli et al., 2016b; Gauthier and van Wassenhove, 2016).

Beyond this overall effect, participants' performance worsened in judging future events in the Past projection, and in judging past events in the Future projection. Such effects, here reported for the first time, could be due to an incompatibility between the Self-Projection and Self-Reference temporal directions. Indeed, when these conditions are opposed, a further cognitive effort would be required, not only to imagine oneself in different time locations, but also to orient oneself towards an opposite time direction. This effort may result in higher switching costs occurring when we refer to two different temporal frames.

More interestingly, in the Post-PA session, we found an improvement in responding to past as compared to future events when participants projected themselves to the Past. The same facilitation was also found when comparing past events in Past and Present projection. We interpreted the improvement toward the Past as a selective effect of the leftwards shift of spatial attention induced by PA. This evidence is consistent with the well-known spatial representation of time (Bonato et al., 2012; Magnani et al., 2014, 2021; Anelli et al., 2015, 2016b; Candini et al., 2022). Further support for the interpretation of visuospatial modulations of PA on MTT comes from the finding that exposure to neutral lenses did not change participants' performance (Control Experiment). Compared to the "canonical" prismatic deviating lenses, the neutral goggles do not deviate the visual field. Therefore, the Control Experiment excludes the possibility that the results from the fMRI experiment could be simply explained by spurious effects due to familiarization or task repetition.

On the functional point of view, a widespread bilateral network was activated during the execution of the MTT task before prism exposure, including fronto-parietal areas, parahippocampal cortices, occipital cortices, basal ganglia and cerebellum. Focusing on the regions of interest (ROIs),

before PA right and left inferior parietal lobules (IPL) were both recruited: the right IPL was activated in the Future projection, whereas the left IPL was activated during the task irrespectively of conditions. These results are in line with Arzy et al. (2009b), who showed that the BOLD signal changed bilaterally in the posterior parietal cortex (PPC) in Self-Projection conditions, arguing that PPC is implicated in both episodic thinking and spatial representation, thus mediating visual imagery during self- and space-related tasks. Using a different paradigm of MTT and a spatial navigation task, Gauthier and vanWassenhove (2016) found a specific activation of a small region of right IPL (BA 39) both in temporal and spatial Self-Projection. Thus, the authors suggested that this sub-region mediates egocentric mapping, required to mentally travel in time and in space.

Furthermore, the Pre-PA ROI analyses revealed the recruitment of left superior temporal gyrus (STG) and left superior frontal gyrus (SFG), especially for the Self-Reference condition. Notably, left STG showed a higher activation when participants classified past events compared to future events, suggesting that this area is involved in accessing past information. In agreement with this view, several studies showed that the left STG (and particularly BA 22) is recruited to successfully recall names (Yagishita et al., 2008) or images (Wu et al., 2020), disclosing its role in memory-related processing. On the other hand, when participants classified future compared to past events, the left superior frontal gyrus (SFG) activation increased. Previous research has suggested that frontal areas play a pivotal role in anticipating future occurrences and decision-making related to the future (Ciaramelli and Di Pellegrino, 2011; Ciaramelli et al., 2021b). In addition, as argued by Arzy at al. (2009b), the frontal lobe is recruited in the future Self-Reference component of MTT "*when transposing one's reference point from self to other, from here to there, and from now to then*" (Arzy et al., 2009b). Our results fit nicely with this view, suggesting that the activity of the left SFG facilitates the processing of future events, regardless of the temporal projection (Anelli et al., 2016b). Alternatively, Gauthier and vanWassenhove (2016) proposed that such a frontal region mediates temporal and spatial ordering of memories. Since these two views

do not exclude each other, here we hypothesize that SFG is required to give a temporal/spatial order to future events. Summarizing, we suggest that right IPL is involved in the Future projection, whereas both left STG and left SFG are involved in Self-Reference, with a complementary role in judging past and future events, regardless of the projection in time.

Looking at the PA modulations on the MTT-related network, in the Post-PA session we observed changes in bilateral IPL and left SFG activity, as well as a selective enhancement of activation in bilateral STG. Then, focusing on the changes induced by PA on parietal regions, ROI analyses showed reduced activity in both left IPL and right IPL. However, the reduction of the left IPL activity was less evident when participants were asked to project themselves to the Past (Self-Projection), suggesting a spared activation of this for Past projection. Thus, we can speculate that such spared activity may reflect the behavioral improvement following PA found in projecting to the Past. Interestingly, the BOLD signal of right IPL correlated with participants' performance: the lower the activity of right IPL, the worse the performance for future events when participants were projected to the Past. Here, we can speculate that this pattern of functional activity in right IPL may indirectly facilitate the access to past events in Past projection, coherently with the behavioral improvement for past, as compared to future events, in the same projection. Overall, this parietal modulation could explain the unbalanced spatial attention towards the past (left of MTL) as a result of PA. In addition, this pattern is in line with an fMRI study by Crottaz-Herbette et al. (2014) showing that a brief exposure to PA induced a bilateral decrease of activation in IPLs when participants performed visuo-spatial and working memory tasks.

When looking at the prefrontal cortex, ROI analysis showed that in Post-PA session the activation of left SFG was overall reduced. More specifically, left SFG showed a greater reduction of the BOLD signal when participants were projected to the Past than to the Future, and a reduced activation when judging future events, confirming previous neuropsychological evidence of a prefrontal involvement in Future Self-Projection and Future Self-Reference (Ciaramelli et al., 2021a; Stendardi et

al., 2021). For instance, Ciaramelli and colleagues (2021a) demonstrated that patients with prefrontal injuries were impaired both in projecting themselves to the Future and in judging future events. This deficit was interpreted as an inability to construct future representations in both components of MTT. In light of this view, we can speculate that the decrease of activation in left SFG due to the PA exposure may resemble the future oriented MTT deficit found in patients with prefrontal damage.

Superior temporal regions were also modulated by the exposure to prismatic lenses, with an enhancement of the BOLD signal in bilateral STG in the Post-PA session. Furthermore, ROI analysis indicated that the right STG increased activity was not related to any MTT condition, thus suggesting a role of STG in maintaining the effects induced by the prism exposure. This hypothesis is in line with results obtained by Luauté et al. (2009) in healthy participants, and by Karnath and colleagues (2001) on patients with neglect as well as in transcranial magnetic stimulation (TMS) studies on healthy participants (Shah-Basak et al., 2018). Considering the involvement in MTT, the ROI analysis on left STG confirmed the engagement of this area in the Self-Reference for past compared to future events, not only in Pre but also in Post PA.

Psycho-physiological interaction (PPI) results showed that left and right IPLs were negatively correlated with left and right STGs after PA, as the activation of both IPLs decreased, the activation of both STGs increased. Coherently with our results, Schintu et al. (2020) found that the resting state functional connectivity (RSFC) was reduced between PPCs and STGs bilaterally after PA. Furthermore, Wilf et al. (2019) showed a reduced connectivity of left IPL with right superior temporal regions following a leftward shift of attention induced by PA. The authors claimed that the decoupling between these areas could be the initial core where the attentional bias towards the left side of space takes place. Interestingly, we also found the activity of left IPL positively correlated with left SFG after PA, suggesting another possible pathway of spatial attention modulation on MTT.

Based on our results and on the previous literature, we suggest an anatomo-functional model that should explain the effects of PA on MTT (Fig. 6). A leftward shift of spatial attention following PA induces, at behavioral level, a facilitation of Past Projection and past events and, at neural level, an effect on both IPLs. This, in turn, activates both STGs and inhibits left SFG. More specifically, we propose that the facilitation of Past Projection may be linked to the bilateral modulation of IPLs activity, while the facilitation of past events is mediated by the inhibition of left SFG and by the increased activation of left STG. Finally, the right STG maintains the PA effects.

In conclusion, our findings and the proposed model shed light on the functional role of the brain areas mediating the effects of spatial attention on our ability to project ourselves in time and to judge whether some events already happened or are expected to happen in the future. Moreover, our results have important implications to further understand the mechanisms underlying the improvement of the neglect deficits following PA, where patients' impairments may concern not only spatial but also a temporal domain. Overall, these findings support the hypothesis of a spatial representation of the subjective timeline. Further work is needed to explore whether such findings following the manipulation of spatial attention on MTT could be also framed within different theoretical models, taking into account other factors mediating the association between time and space.

Before concluding, it is worth noticing some limitations of our study. Firstly, we did not control for the rightward shift of spatial attention. We selected the leftward attentional shift as our focus, given our primary aim to identify the brain structures underpinning the PA effects on MTT in the healthy population as a preliminary step, with the aim to build an anatomo-functional model that will be also tested in patients with left neglect. Nevertheless, further research is necessary to assess the effects on MTT and their neural substrates of the rightward shift of spatial attention in the healthy population and in neuropsychological patients. Another limitation of the present study consists in not considering personal or non-personal categorization of the events as factors in the analyses. Since this is a relevant

component in MTT ability, future studies will address this issue investigating the effects of PA on personal and non-personal events. Moreover, we only tested young participants because different age groups may adopt different temporal perspectives when making judgments about the events used in the MTT task. Further research on older adults will be necessary to clarify how aging affects the ability to MTT and its associated functional correlates. Lastly, we would like to point out that this study was conducted with a limited sample of Western participants. Previous research has shown that the representation of time can be influenced by culture, and different effects of PA on MTT have been observed in individuals from diverse cultural backgrounds, particularly those with distinct reading and writing systems (Anelli et al. 2018). Future research involving a larger sample, including participants from different cultural backgrounds, will be essential for a comprehensive model of the MTT-related neural correlates and their modulation after shift of attention.

References

Addis, D. R., Wong, A. T., and Schacter, D. L. (2007). Remembering the past and imagining the future: Common and distinct neural substrates during event construction and elaboration. *Neuropsychologia* 45, 1363–1377. doi: 10.1016/j.neuropsychologia.2006.10.016.

Albini, F., Pisoni, A., Salvatore, A., Calzolari, E., Casati, C., Marzoli, S. B., Falini, A., Crespi, S. A., Godi, C., Castellano, A., Bolognini, N., & Vallar, G. (2022). Aftereffects to Prism Exposure without Adaptation: A Single Case Study. *Brain Sciences*, 12(4), 480. doi: 10.3390/brainsci12040480

Anelli, F., Avanzi, S., Arzy, S., Mancuso, M., and Frassinetti, F. (2018). Effects of spatial attention on mental time travel in patients with neglect. *Cortex* 101, 192–205. doi: 10.1016/j.cortex.2018.01.012.

Anelli, F., Candini, M., Cappelletti, M., Oliveri, M., and Frassinetti, F. (2015). The remapping of time by active tool-use. *PLoS One* 10, 1–13. doi: 10.1371/journal.pone.0146175.

Anelli, F., Ciaramelli, E., Arzy, S., and Frassinetti, F. (2016a). Age-Related Effects on Future Mental Time Travel. *Neural Plast* 2016. doi: 10.1155/2016/1867270.

Anelli, F., Ciaramelli, E., Arzy, S., and Frassinetti, F. (2016b). Prisms to travel in time: Investigation of time-space association through prismatic adaptation effect on mental time travel. *Cognition* 156, 1–5. doi: 10.1016/j.cognition.2016.07.009.

Anelli, F., Peters-Founshtein, G., Shreibman, Y., Moreh, E., Forlani, C., Frassinetti, F., Arzy, S. (2018). Nature and nurture effects on the spatiality of the mental time line. *Scientific Reports* 8. doi: 10.1038/s41598-018-29584-3

Anelli, F., and Frassinetti, F. (2019). Prisms for timing better: A review on application of prism adaptation on temporal domain. *Cortex* 119, 583–593. doi: 10.1016/j.cortex.2018.10.017.

Arzy, S., Adi-Japha, E., and Blanke, O. (2009a). The mental time line: An analogue of the mental number line in the mapping of life events. *Conscious Cogn* 18, 781–785. doi: 10.1016/j.concog.2009.05.007.

Arzy, S., Collette, S., Ionta, S., Fornari, E., and Blanke, O. (2009b). Subjective mental time: The functional architecture of projecting the self to past and future. *European Journal of Neuroscience* 30, 2009–2017. doi: 10.1111/j.1460-9568.2009.06974.x.

Arzy, S., Molnar-Szakacs, I., and Blanke, O. (2008). Self in time: Imagined self-location influences neural activity related to mental time travel. *Journal of Neuroscience* 28, 6502–6507. doi: 10.1523/JNEUROSCI.5712-07.2008.

Bonato, M., Saj, A., and Vuilleumier, P. (2016). Hemispatial Neglect Shows That "Before" Is "Left." *Neural Plast* 2016. doi: 10.1155/2016/2716036.

Bonato, M., Zorzi, M., and Umiltà, C. (2012). When time is space: Evidence for a mental time line. *Neurosci Biobehav Rev* 36, 2257–2273. doi: 10.1016/j.neubiorev.2012.08.007.

Brett, M., Anton, J. L., Valabregue, R., and Jean-Baptiste, P. (2002). Region of interest analysis using an SPM toolbox. *Neuroimage* 16.

Buckner, R. L., and Carroll, D. C. (2007). Self-projection and the brain. *Trends Cogn Sci* 11, 49–57. doi: 10.1016/j.tics.2006.11.004.

Candini, M., D'Angelo, M., and Frassinetti, F. (2022). Time Interaction with Two Spatial Dimensions: From Left/Right to Near/Far. *Front Hum Neurosci* 15, 1–11. doi: 10.3389/fnhum.2021.796799.

Casadio, C., Patané, I., Candini, M., Lui, F., Frassinetti, F., Benuzzi, F. (under review) Effects of the perceived temporal distance of events on Mental Time Travel and its underlying brain circuits.

Ciaramelli, E., Anelli, F., and Frassinetti, F. (2021a). An asymmetry in past and future mental time travel following vmPFC damage. *Soc Cogn Affect Neurosci* 16, 315–325. doi: 10.1093/scan/nsaa163.

Ciaramelli, E., De Luca, F., Kwan, D., Mok, J., Bianconi, F., Knyagnytska, V., et al. (2021b). The role of ventromedial prefrontal cortex in reward valuation and future thinking during intertemporal choice. *Elife* 10, 1–17. doi: 10.7554/ELIFE.67387.

Ciaramelli, E., and Di Pellegrino, G. (2011). Ventromedial prefrontal cortex and the future of morality. *Emotion Review* 3, 308–309. doi: 10.1177/1754073911402381.

Crottaz-Herbette, S., Fornari, E., and Clarke, S. (2014). Prismatic adaptation changes visuospatial representation in the inferior parietal lobule. *Journal of Neuroscience* 34, 11803–11811. doi: 10.1523/JNEUROSCI.3184-13.2014.

Dafni-Merom, A., and Arzy, S. (2020). The radiation of autonoetic consciousness in cognitive neuroscience: A functional neuroanatomy perspective. *Neuropsychologia* 143. doi: 10.1016/j.neuropsychologia.2020.107477.

D'argembeau, A. (2020). Zooming in and out on one's life: Autobiographical representations at multiple time scales. *J Cogn Neurosci* 32, 2037–2055. doi: 10.1162/jocn_a_01556.

Fellows, L. K., and Farah, M. J. (2005). Dissociable elements of human foresight: A role for the ventromedial frontal lobes in framing the future, but not in discounting future rewards. *Neuropsychologia* 43, 1214–1221. doi: 10.1016/j.neuropsychologia.2004.07.018.

Frassinetti, F., Angeli, V., Meneghello, F., Avanzi, S., and Làdavas, E. (2002). Long-lasting amelioration of visuospatial neglect by prism adaptation. *Brain* 125, 608–623. doi: 10.1093/brain/awf056.

Friston, K. (2012). Ten ironic rules for non-statistical reviewers. *Neuroimage* 61, 1300–1310. doi: 10.1016/j.neuroimage.2012.04.018.

Garcia-Pelegrin, E., Wilkins, C., and Clayton, N. S. (2021). The Ape That Lived to Tell the Tale. The Evolution of the Art of Storytelling and Its Relationship to Mental Time Travel and Theory of Mind. *Front Psychol* 12, 1–15. doi: 10.3389/fpsyg.2021.755783.

Gauthier, B., Pestke, K., and Van Wassenhove, V. (2019). Building the Arrow of Time.. over Time: A Sequence of Brain Activity Mapping Imagined Events in Time and Space. *Cerebral Cortex* 29, 4398–4414. doi: 10.1093/cercor/bhy320.

Gauthier, B., and van Wassenhove, V. (2016). Time is not space: Core computations and domain-specific networks for mental travels. *Journal of Neuroscience* 36, 11891–11903. doi: 10.1523/JNEUROSCI.1400-16.2016.

Gilbert, D. T., and Wilson, T. D. (2007). Prospection: Experiencing the Future. *Science (1979)* 317, 1351–1355.

JASP Team (2023). JASP (Version 0.17.3) [Computer software].

Karnath, H. O., Ferber, S., and Himmelbach, M. (2001). Spatial awareness is a function of the temporal not the posterior parietal lobe. *Nature* 411, 950–3.

Koch, G., Oliveri, M., Cheeran, B., Ruge, D., Gerfo, E. L., Salerno, S., et al. (2008). Hyperexcitability of parietal-motor functional connections in the intact left-hemisphere of patients with neglect. *Brain* 131, 3147–3155. doi: 10.1093/brain/awn273.

Lakoff, G., and Johnson, M. (1999). *Philosophy in the Flesh: The Embodied Mind and Its Challenge to Western Thought*. New York: Basic Book.

Luauté, J., Schwartz, S., Rossetti, Y., Spiridon, M., Rode, G., Boisson, D., et al. (2009). Dynamic changes in brain activity during prism adaptation. *Journal of Neuroscience* 29, 169–178. doi: 10.1523/JNEUROSCI.3054-08.2009.

Magnani, B., Frassinetti, F., Ditye, T., Oliveri, M., Costantini, M., and Walsh, V. (2014). Left insular cortex and left SFG underlie prismatic adaptation effects on time perception: Evidence from fMRI. *Neuroimage* 92, 340–348. doi: 10.1016/j.neuroimage.2014.01.028.

Magnani, B., Mangano, G. R., Frassinetti, F., and Oliveri, M. (2013). The role of posterior parietal cortices on prismatic adaptation effects on the representation of time intervals. *Neuropsychologia* 51, 2825–2832. doi: 10.1016/j.neuropsychologia.2013.08.006.

Magnani, B., Musetti, A., and Frassinetti, F. (2021). Neglect in temporal domain: Amelioration following a prismatic adaptation treatment and implications in everyday life. A single case study. *Brain Cogn* 150, 105712. doi: 10.1016/j.bandc.2021.105712.

Mathworks (n.d.). MatLab.

Newport, R., and Schenk, T. (2012). Prisms and neglect: What have we learned? *Neuropsychologia* 50, 1080–1091. doi: 10.1016/j.neuropsychologia.2012.01.023.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia* 9, 97–113. doi: 10.1016/0028-3932(71)90067-4.

Oliveri, M., Koch, G., and Caltagirone, C. (2009). Spatial-temporal interactions in the human brain. *Exp Brain Res* 195, 489–497. doi: 10.1007/s00221-009-1834-1.

Ouellet, M., Santiago, J., Funes, M. J., and Lupiáñez, J. (2010). Thinking about the future moves attention to the right. *J Exp Psychol Hum Percept Perform* 36, 17–24. doi: 10.1037/a0017176.

Panico, F., Rossetti, Y., and Trojano, L. (2020). On the mechanisms underlying Prism Adaptation: A review of neuro-imaging and neuro-stimulation studies. *Cortex* 123, 57–71. doi: 10.1016/j.cortex.2019.10.003.

Patané, I., Farnè, A., and Frassinetti, F. (2016). Prismatic Adaptation Induces Plastic Changes onto Spatial and Temporal Domains in Near and Far Space. *Neural Plast* 2016. doi: 10.1155/2016/3495075.

Pisella, L., Rode, G., Farnè, A., Tilikete, C., and Rossetti, Y. (2006). Prism adaptation in the rehabilitation of patients with visuo-spatial cognitive disorders. *Curr Opin Neurol* 19, 534–542. doi: 10.1097/WCO.0b013e328010924b.

Redding, G. M., and Wallace, B. (2006). Prism adaptation and unilateral neglect: Review and analysis. *Neuropsychologia* 44, 1–20. doi: 10.1016/j.neuropsychologia.2005.04.009.

Rode, G., Pagliari, C., Huchon, L., Rossetti, Y., and Pisella, L. (2017). Semiology of neglect: An update. *Ann Phys Rehabil Med* 60, 177–185. doi: 10.1016/j.rehab.2016.03.003.

Rode, G., Rossetti, Y., and Boisson, D. (2001). Prism adaptation improves representational neglect. *Neuropsychologia* 39, 1250–1254. doi: 10.1016/S0028-3932(01)00064-1.

Rossetti, Y., Rode, G., Pisella, L., Farné, A., Li, L., Boisson, D., et al. (1998). Prism adaptation to a rightward optical deviation rehabilitates left hemispatial neglect. *Nature* 395, 166–169. doi: 10.1038/25988.

Santiago, J., Lupáñez, J., Pérez, E., and Funes, M. J. (2007). Time (also) flies from left to right. *Psychon Bull Rev* 14, 512–516. doi: 10.3758/BF03194099.

Schacter, D. L., and Addis, D. R. (2007). The cognitive neuroscience of constructive memory: Remembering the past and imagining the future. *Philosophical Transactions of the Royal Society B: Biological Sciences* 362, 773–786. doi: 10.1098/rstb.2007.2087.

Schintu, S., Freedberg, M., Gotts, S. J., Cunningham, C. A., Alam, Z. M., Shomstein, S., et al. (2020). Prism adaptation modulates connectivity of the intraparietal sulcus with multiple brain networks. *Cerebral Cortex* 30, 4747–4758. doi: 10.1093/cercor/bhaa032.

Schintu, S., Patané, I., Caldano, M., Salemme, R., Reilly, K. T., Pisella, L., et al. (2017). The asymmetrical effect of leftward and rightward prisms on intact visuospatial cognition. *Cortex* 97, 23–31. doi: 10.1016/j.cortex.2017.09.015.

Serino, A., Bonifazi, S., Pierfederici, L., and Làdavas, E. (2007). Neglect treatment by prism adaptation: What recovers and for how long. *Neuropsychol Rehabil* 17, 657–687. doi: 10.1080/09602010601052006.

Shah-Basak, P. P., Chen, P., Caulfield, K., Medina, J., and Hamilton, R. H. (2018). The role of the right superior temporal gyrus in stimulus-centered spatial processing. *Neuropsychologia* 113, 6–13. doi: 10.1016/j.neuropsychologia.2018.03.027.

Stendardi, D., Biscotto, F., Bertossi, E., and Ciaramelli, E. (2021). Present and future self in memory: the role of vmPFC in the self-reference effect. *Soc Cogn Affect Neurosci* 16, 1205–1213. doi: 10.1093/scan/nsab071.

Suddendorf, T., and Corballis, M. C. (2007). The evolution of foresight: What is mental time travel, and is it unique to humans? *Behavioral and Brain Sciences* 30, 299–351. doi: 10.1017/S0140525X07001975.

Terruzzi, S., Crivelli, D., Pisoni, A., Mattavelli, M., Romero Lauro, L. J., Bolognini, N., Vallar, G. (2021). The role of the right posterior parietal cortex in prism adaptation and its aftereffects. *Neuropsychologia* 150, 107672. doi: 10.1016/j.neuropsychologia.2020.107672.

TIBCO Software Inc. (2020). Data Science Workbench, version 14. http://tibco.com.

Torralbo, A., Santiago, J., and Lupiáñez, J. (2006). Flexible Conceptual Projection of Time Onto Spatial Frames of Reference. *Cogn Sci* 30, 745–757. doi: 10.1207/s15516709cog0000_67.

Wilf, M., Serino, A., Clarke, S., and Crottaz-Herbette, S. (2019). Prism adaptation enhances decoupling between the default mode network and the attentional networks. *Neuroimage* 200, 210–220. doi: 10.1016/j.neuroimage.2019.06.050.

Wu, D., Chen, T., Huang, X., Chen, L., Yue, Y., Yang, H., et al. (2020). The Role of Old Photos in Reminiscence Therapy in Elderly Women With Depressive Symptoms: A Functional Magnetic Resonance Imaging Study. *Biol Res Nurs* 22, 234–246. doi: 10.1177/1099800420908002.

Yagishita, S., Watanabe, T., Asari, T., Ito, H., Kato, M., Ikehira, H., et al. (2008). Role of left superior temporal gyrus during name recall process: An event-related fMRI study. *Neuroimage* 41, 1142–1153. doi: 10.1016/j.neuroimage.2008.03.008.

Table 1

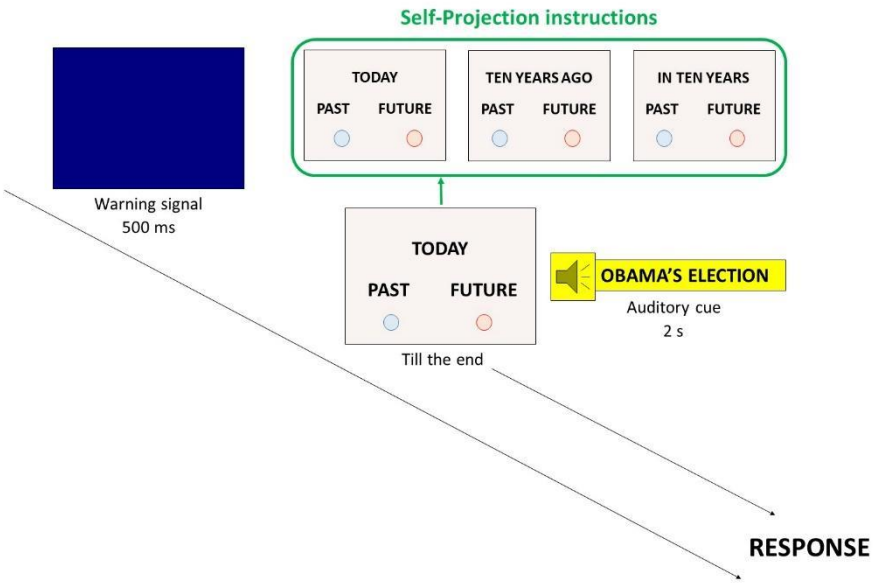
Activations in Post-PA>Pre-PA contrast.

Anatomical region	BA	side	K	Z_E	Spatial coordinates (MNI)		
					x	y	z
Superior Temporal Gyri	41, 22	r	125	5.50	45	-22	5
				3.61	51	-31	11
		l	111	4.47	-45	-19	2
				4.26	-42	-25	11
				4.06	-39	-34	8

Note: Areas of increased signal for the Post-PA>Pre-PA contrast (cluster size k>109, corrected at α<0.05). BA = Broadman Area, r= right, l= left.

Figure 1

Example of a single trial



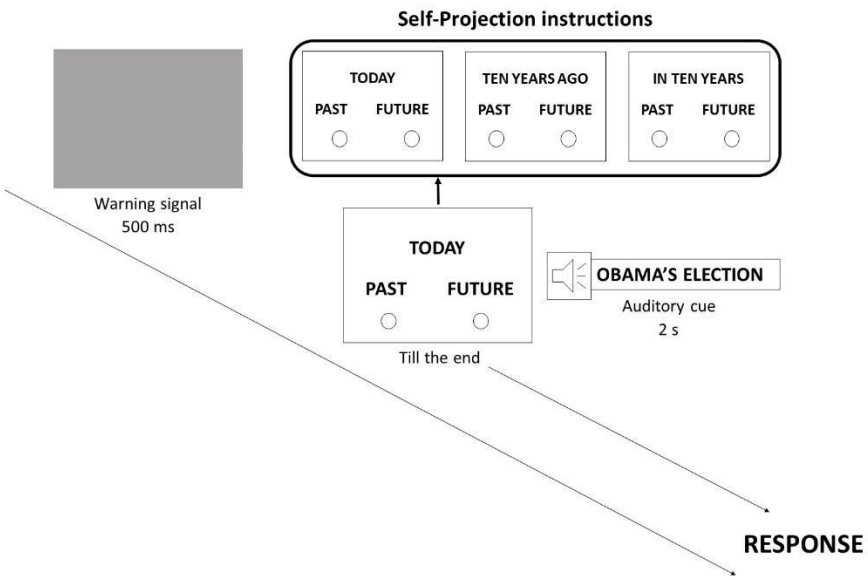
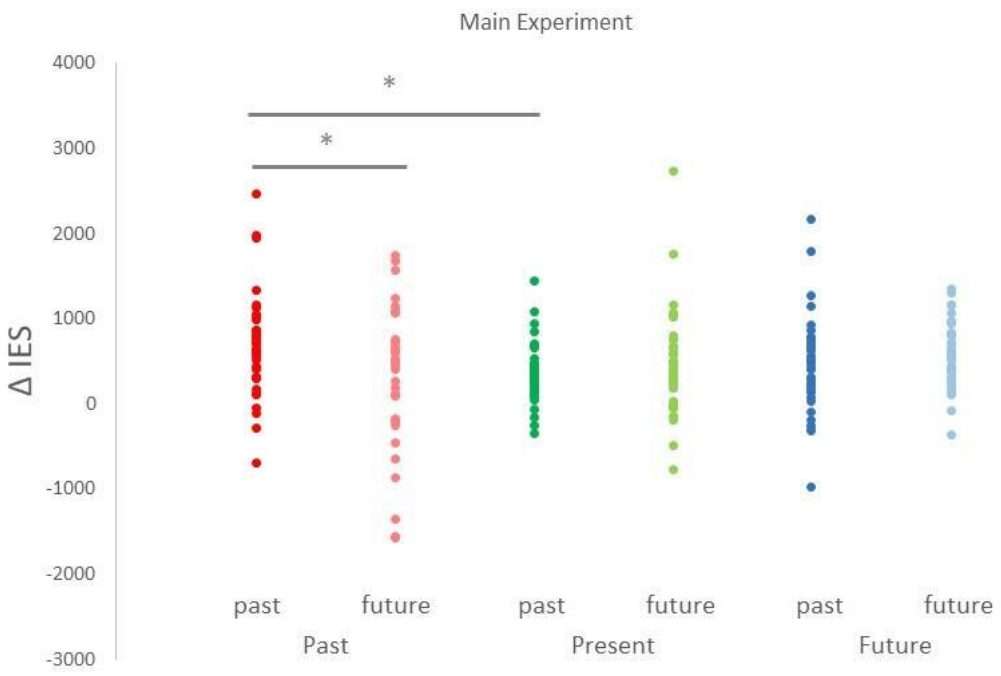


Figure 1: The temporal sequence of a single trial in the MTT task with an example of the three possible Self-Projections (past, present, future).

Figure 2

Behavioral results of the Main Experiment



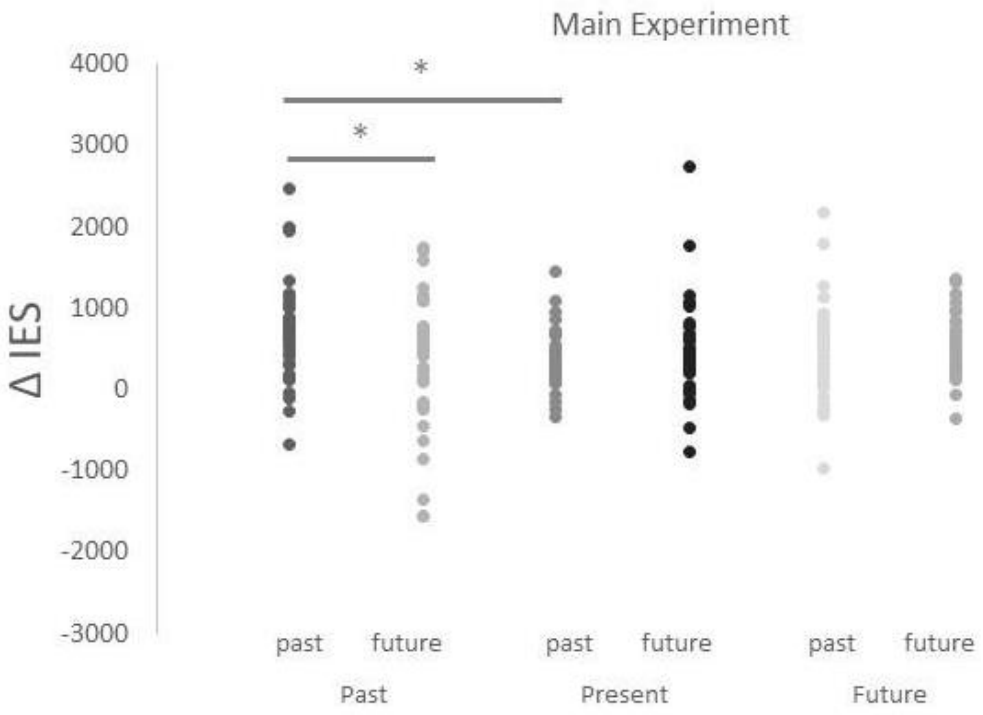


*Figure 2: The Self-Projection*Self-Reference interaction on delta Inverse Efficiency Score (Δ IES). Δ IES values were calculated subtracting IES for Post-PA from IES for Pre-PA. The higher the Δ IES values, the better the performance after PA. Dark and light colors indicate past and future Self-Reference respectively. Asterisks indicate significant differences (p<0.05).*

Figure 3

Pre-PA session functional results

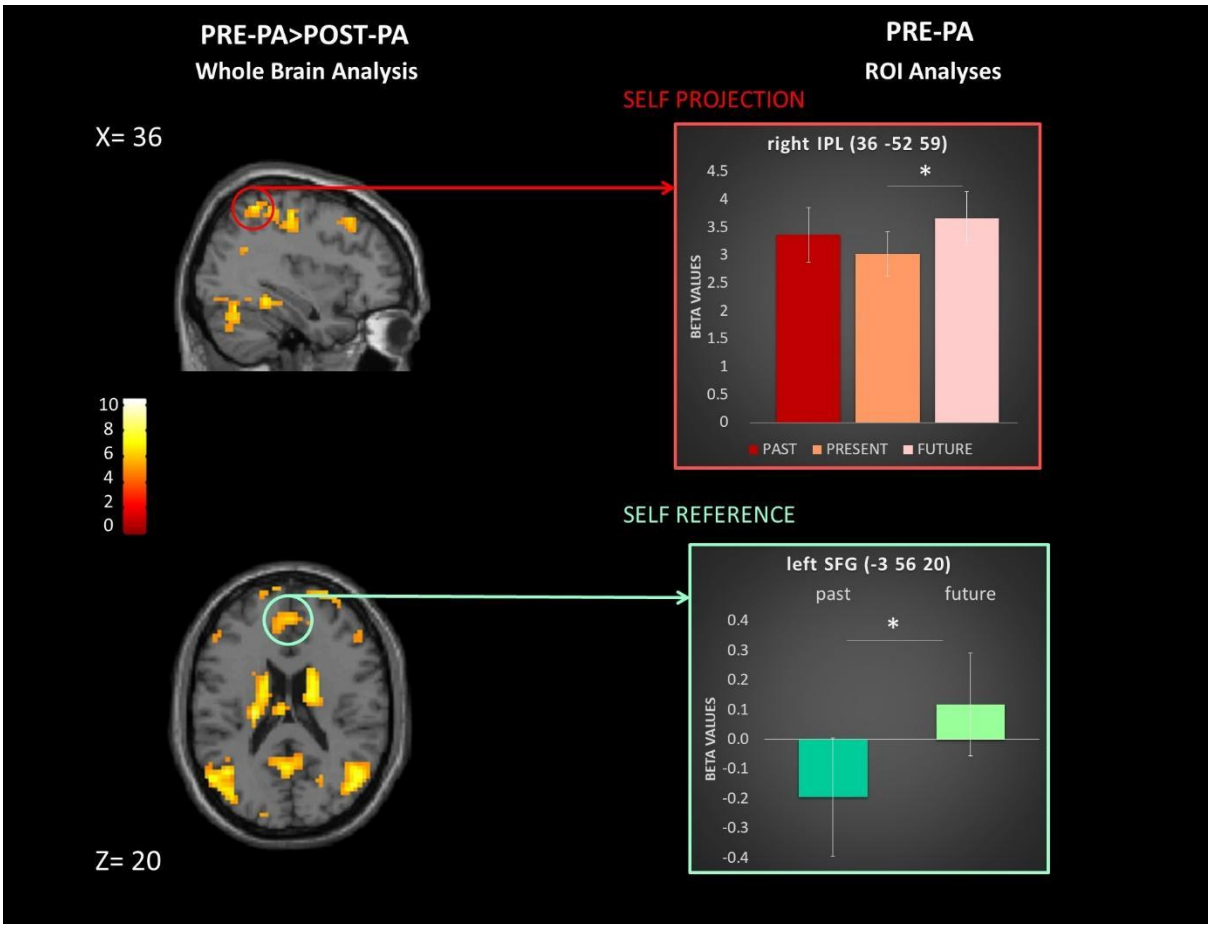


Figure 3: (A – left) Activations in Pre-PA>Post-PA contrast p<0.05 FWE corrected k>0, displaying only clusters >10. (B - right) Bar plots represent ROI analyses results as a function of MTT conditions (Self-Reference in green and Self-Projection in red). Error bars depict standard errors of the mean (SEM). Asterisks indicate significant differences (p<0.05).

Figure 4

Post-PA session functional results

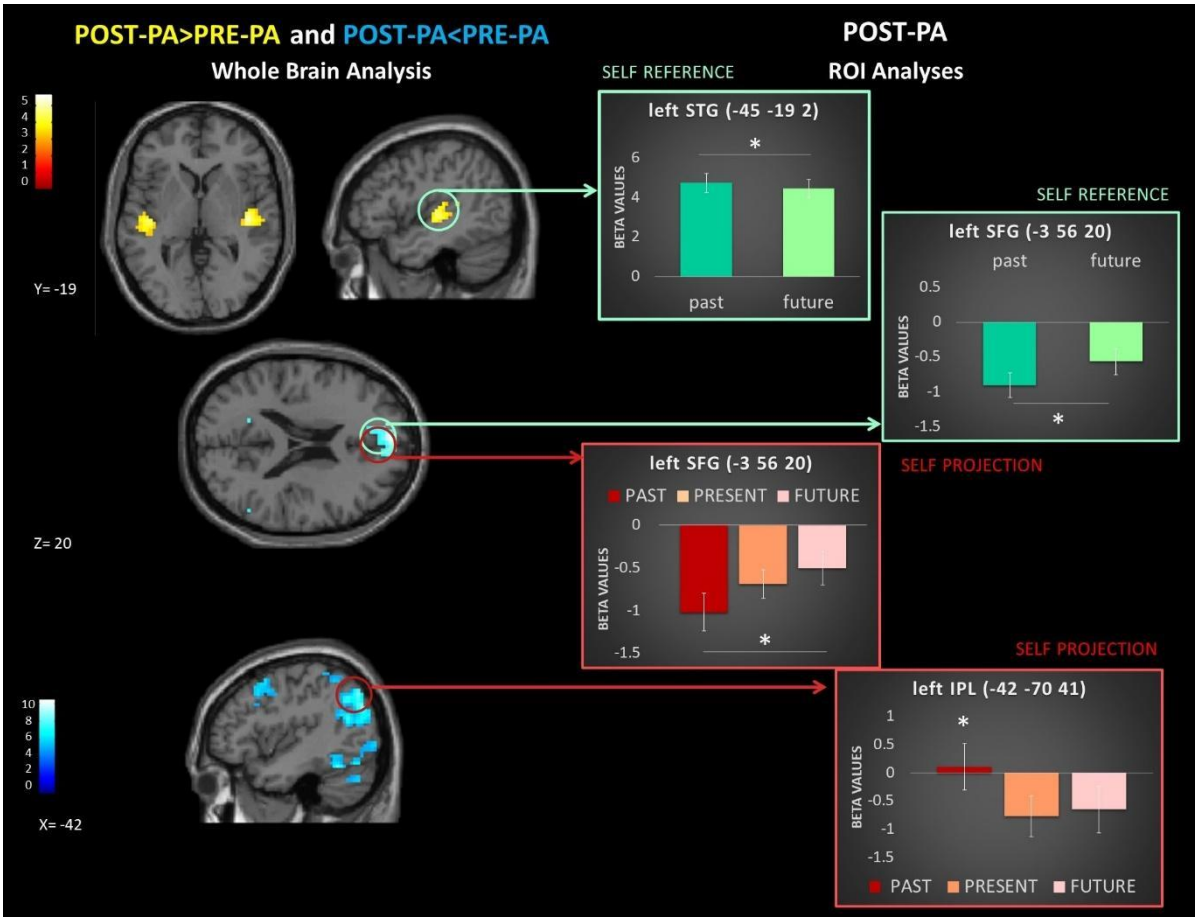


Figure 4: (A - left) Activations in Post-PA>Pre-PA and Reduction of activation (yellow blobs) in Post-PA<Pre-PA contrast cluster size k>109, corrected at α<0.05 (blue blobs). (B - right) Bar plots represent ROI analyses results in the Post-PA session as a function of MTT conditions (Self-Reference in green and Self-Projection in red). Error bars depict standard errors of the mean (SEM). Asterisks indicate significant differences (p<0.05).

Figure 5

ROI analyses results

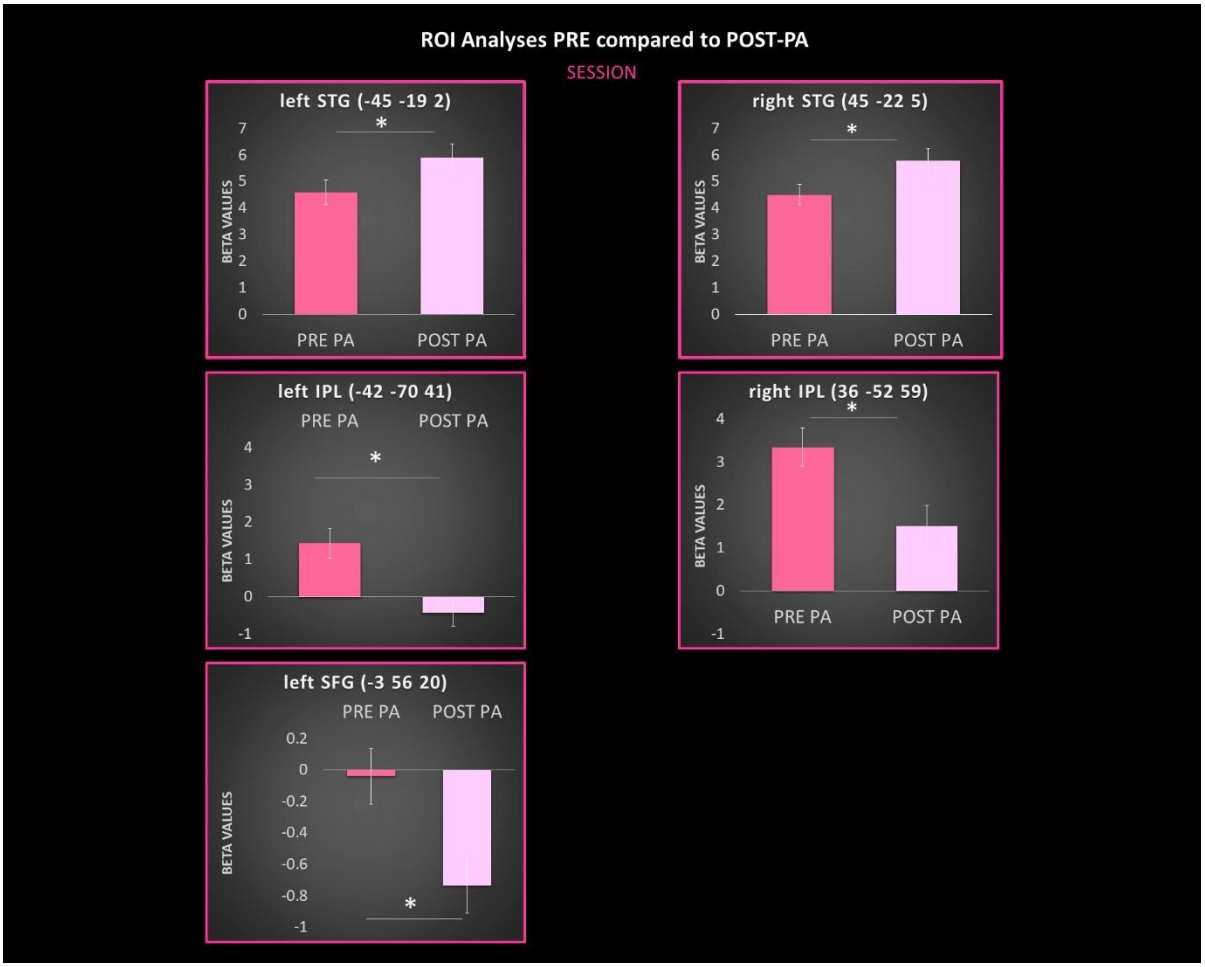
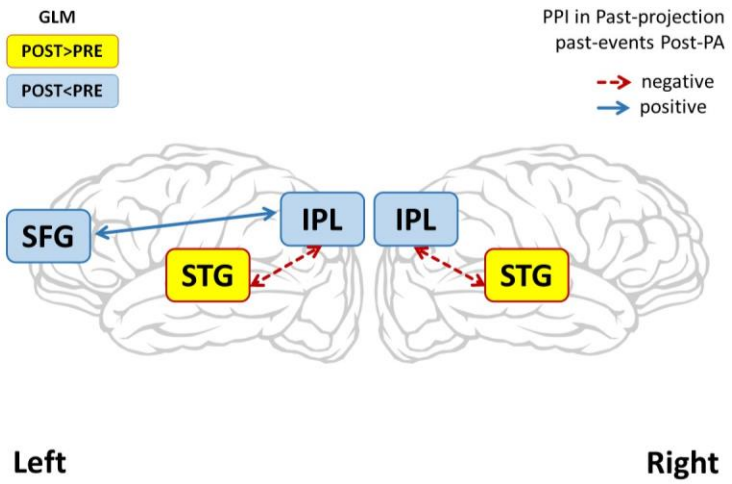


Figure 5: Session main effect in ROI analyses. Error bars depict standard errors of the mean (SEM). Asterisks indicate significant differences (p<0.05).

Figure 6

Anatomo-functional model



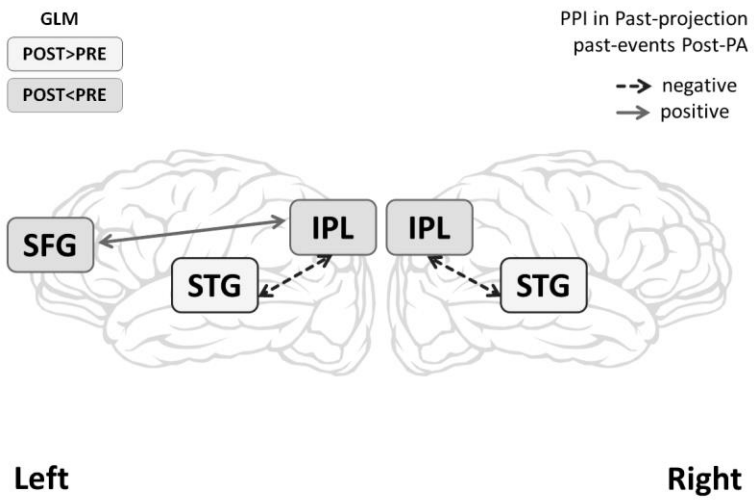


Figure 6: Model of PA effects on an attentional network during MTT when judging past events in Past projection. IPL= Inferior Parietal Lobule, STG= Superior Temporal Gyrus, SFG= Superior Frontal Gyrus. Boxes represent the results of the GLM analysis: POST>PRE = brain areas showing increased activation in the post PA session compared to the pre PA (in light blue). POST<PRE = brain areas showing increased activation in the pre PA session compared to the post PA (in yellow). Arrows indicate the results of the

psycho-physiological interactions analysis: dotted arrows (in red) indicate a negative PPI; solid arrow (in blue) indicates a positive PPI.