



# Supramodal effect of rightward prismatic adaptation on spatial representations within the ventral attentional system

Isabel Tissieres<sup>1</sup> · Eleonora Fornari<sup>2</sup> · Stephanie Clarke<sup>1</sup> · Sonia Crottaz-Herbette<sup>1</sup> 

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## Abstract

Rightward prismatic adaptation (R-PA) was shown to alleviate not only visuo-spatial but also auditory symptoms in neglect. The neural mechanisms underlying the effect of R-PA have been previously investigated in visual tasks, demonstrating a shift of hemispheric dominance for visuo-spatial attention from the right to the left hemisphere both in normal subjects and in patients. We have investigated whether the same neural mechanisms underlie the supramodal effect of R-PA on auditory attention. Normal subjects underwent a brief session of R-PA, which was preceded and followed by an fMRI evaluation during which subjects detected targets within the left, central and right space in the auditory or visual modality. R-PA-related changes in activation patterns were found bilaterally in the inferior parietal lobule. In either modality, the representation of the left, central and right space increased in the left IPL, whereas the representation of the right space decreased in the right IPL. Thus, a brief exposure to R-PA modulated the representation of the auditory and visual space within the ventral attentional system. This shift in hemispheric dominance for auditory spatial attention offers a parsimonious explanation for the previously reported effects of R-PA on auditory symptoms in neglect.

**Keywords** Supramodal · Prismatic adaptation · Functional MRI · Ventral attentional system · Inferior parietal lobule

## Abbreviations

AG	Angular gyrus
PSC	Percent signal changes
fMRI	Functional magnetic resonance imaging
IPL	Inferior parietal lobule
R-PA	Rightward prismatic adaptation
L-PA	Leftward prismatic adaptation
SMG	Supramarginal gyrus

## Introduction

Rightward prismatic adaptation (R-PA) was repeatedly shown to alleviate visuo-spatial symptoms in neglect (Rossetti et al. 1998; Redding and Wallace 2006; Pisella et al. 2006; Rode et al. 2007; Danckert et al. 2008; Fortis et al. 2011; Yang et al. 2013; Jacquin-Courtois et al. 2013). In addition, it was reported to lessen auditory symptoms by reducing left ear extinction in dichotic listening (Jacquin-Courtois et al. 2010; Tissieres et al. 2017) and by improving the detection of auditory targets (Eramudugolla et al. 2010). These latter observations suggest that R-PA may have a supramodal effect. The mechanism by which R-PA affects spatial attention is partially understood in the visual but not in the auditory modality (e.g., Clarke and Crottaz-Herbette 2016).

Prismatic adaptation is a visuo-motor training task during which subjects point to visual targets while wearing glasses mounted with prisms. In neglect rehabilitation, the prisms deviate the visual field to the right. During the initial trials, subjects show pointing errors in the direction of the prism deviation, then they adapt their movement and point correctly to the target. When the prisms are removed, the first trials show pointing errors in the opposite direction to the

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✉ Sonia Crottaz-Herbette  
sonia.crottaz-herbette@chuv.ch

<sup>1</sup> Neuropsychology and Neurorehabilitation Service, Centre Hospitalier Universitaire Vaudois (CHUV), University of Lausanne, Av. Pierre-Decker 5, 1011 Lausanne, Switzerland

<sup>2</sup> CIBM (Centre d'Imagerie Biomédicale), Department of Radiology, Centre Hospitalier Universitaire Vaudois (CHUV), University of Lausanne, 1011 Lausanne, Switzerland

prism deviation (Rossetti et al. 1998). The neural mechanisms underlying the effect of R-PA have been investigated in visual tasks. In normal subjects, several studies revealed the involvement of the right posterior parietal cortex and in the right cerebellum during the stages of the visuo-motor adaptation (Clower et al. 1996; Danckert et al. 2008; Luauté et al. 2009; Chapman et al. 2010; Küper et al. 2014). By comparing task-related brain activations before and after prismatic adaptation in normal subjects, Crottaz-Herbette and colleagues have shown that R-PA modulates visuo-spatial representations bilaterally in the inferior parietal lobules (IPL) by increasing the representation of the left, center and right visual field in the left IPL and decreasing the representation of the right visual field in the right IPL (Crottaz-Herbette et al. 2014). Using the same paradigm in neglect, R-PA was found to enhance the representation of left and central visual space within the left hemisphere in IPL and in parts of the temporal and prefrontal convexities (Crottaz-Herbette et al. 2017a). Thus, R-PA shifts the hemispheric dominance for visuo-spatial attention from the right to the left hemisphere (Clarke and Crottaz-Herbette 2016). In contrast, L-PA was found to enhance the representation of the right visual space within the right IPL (Crottaz-Herbette et al. 2017b); this change offers a partial explanation for the attentional bias towards the right space, which is characteristic of the pseudo-neglect induced by L-PA in normal subjects (Colent et al. 2000; Michel 2003; Martín-Arévalo et al. 2016).

Auditory spatial processing relies heavily on the dorsal auditory pathway and more particularly on IPL (Maeder et al. 2001; Arnott et al. 2004; Brunetti et al. 2005; Deouell et al. 2007; Häkkinen et al. 2015). Several lines of evidence support right-hemispheric dominance for auditory spatial functions. In particular, the right IPL was shown to be competent for the whole auditory space, as demonstrated in activation (Bushara et al. 1999; Kaiser et al. 2000; Itoh et al. 2000; De Santis et al. 2007) and lesion studies (Tanaka et al. 1999; Spierer et al. 2009). In contrast, the left IPL is limited to the representation of the contralateral, right auditory hemisphere, as reported in EEG (Kaiser et al. 2000; Spierer et al. 2008), transcranial magnetic stimulation (Lewald et al. 2002) and lesion studies (Clarke et al. 2000; Spierer et al. 2009). The regions, which are involved in auditory spatial processing, are partially co-extensive with regions involved in visuo-spatial functions; this is the case of parts of the right IPL, this latter has been proposed to be involved in multimodal spatial processing (Bushara et al. 1999).

The contiguity of visual and auditory spatial processing units within the right IPL suggests that similar neural mechanisms may underlie the effect of R-PA in both modalities. If so, R-PA is likely to switch hemispheric dominance not only of visual but also of auditory spatial representation from the right to the left IPL. We have tested this hypothesis

by comparing pre- and post-R-PA activation patterns elicited by auditory or visual stimuli presented in the left, central or right space in a between-subjects design. Activation data were analyzed with a mixed-design ANOVA, with Session (pre, post R-PA) and Stimulus position (left, center, right) as within-subject factors and Modality (visual, auditory) as between-subjects factor. Four specific issues were investigated. First, we have expected that R-PA has a general impact on the processing within the left and right IPL, independently of the modality. This was indeed demonstrated by a massive main effect of Session. Second, R-PA was expected to increase the representation of the ipsilateral space within the left IPL and to decrease it within the right IPL. This change was revealed by the interaction of the factors Stimulus position and Session, independently of the modality. Third, the modulation by R-PA in the IPL may differ between modalities. If so, we would expect a significant interaction between the factor Modality and Session, which in fact did not occur within the IPL on either side. Fourth, we have expected that R-PA modulates spatial representations in either modality in the IPL. This was demonstrated by a significant main effect of Session in the IPL for each modality separately.

## Materials and methods

### Participants

Thirty healthy right-handed (Oldfield 1971) subjects participated in this study (16 in the auditory task: 8 men, mean age = 27.7 years, standard deviation (SD) = 4.3 years; and 14 in the visual task: 7 men, mean age = 26 years, SD = 5 years). None of the subjects had a history of psychiatric or neurological disorder; all reported normal or corrected-to-normal vision and normal hearing. The study has been approved by the Ethic Committee of the Canton de Vaud, Switzerland and all subjects provided written informed consent according to the procedures.

### Experimental design

The experiment consisted of three parts: (1) the pre R-PA MRI session; (2) R-PA; and (3) the post R-PA MRI Session. Subjects started the experiment by anatomical MRI sequences and fMRI acquisitions of the auditory or the visual detection task. Other anatomical and functional sequences were acquired for the purpose of another study, but are not reported here. Then subjects underwent a R-PA session outside the scanner room. After the R-PA session, subjects had a second fMRI session, repeating the same task as before the R-PA (i.e., the visual or auditory detection task). As in the previous study (Crottaz-Herbette et al.

2014), the order of tasks within the pre- and post-PA fMRI sessions was counterbalanced across subjects. In addition, the same time schedule was used, for which the adaptation effects were shown to be preserved throughout the time span of the post-PA fMRI acquisition (Crottaz-Herbette et al. 2014).

### Auditory detection task

The design of the auditory task was similar to the design used in our previous visual task (Crottaz-Herbette et al. 2014). It was used to reveal changes in the spatiotopic representation of sounds and hence it was important that performance remained as constant as possible before and after the R-PA session. Auditory stimuli were bursts of pink noise presented for 500 ms. Sounds onset and offset were ramped with 10 ms of a linear slope. Broadband noise was chosen because it was proven to be better for localization tasks than tones (Recanzone 2000). Three different positions were used: 30° to the left of the medio-sagittal plane, the medio-sagittal plane (0°) or 30° to the right of the medio-sagittal plane; the three positions were easily discriminated by all subjects. Sounds were elaborated using interaural level differences (ILD): a difference of 4 dB between left and right channels was used to create stimuli at 30° to the left or to the right. A sound without intensity difference between the two channels was used to create central stimuli. Sounds were created using Audacity 2.1.0 (<http://audacity.sourceforge.net/>). Positions of the stimuli were pseudo-randomized; each sound was presented 20 times. The inter-event intervals were jittered and lasted up to 20 s with a step of 1 s. The total task length was 6 min 44 s. During the task, subjects had to maintain their gaze straight-ahead by looking at a red cross in the center of the screen. Subjects were asked to press on a button with their right index when a target was detected. The task was developed using E-Prime 2.0 (Psychology Software Tools, Inc.).

### Visual detection task

The visual task and corresponding fMRI and behavioral data came from our previous study (Crottaz-Herbette et al. 2014), however, the whole set of fMRI data were reprocessed in the same way as the newly acquired auditory detection task (see data analysis below). Visual stimuli were large white stars on a black background, presented for 500 ms in three different positions: in the midsagittal plane, at 20° to the right or 20° to the left. The positions of the stimuli were pseudo-randomized and each of them was presented 20 times. The jitter of inter-event intervals was up to 20 s with a step of 1 s. The duration of the task was 6 min 44 s. A red cross in the center of the screen helped subjects to maintain their gaze straight-ahead. Subjects pressed on a button with their right

index when they detected a target. E-Prime 2.0 (Psychology Software Tools, Inc.) was used to develop the task.

### Prismatic adaptation

Participants underwent a R-PA session outside the scanner. The adaptation consisted of 3 min (around 150 movements) of pointing with the right index to two black dots presented at a distance of 57 cm and 14° to the left or to the right of their midsagittal plane. Their head was positioned on a chinrest and the first two-thirds of the pointing trajectories were hidden from their sight. During these movements, all participants wore prisms (<http://www.optiquepeter.com>) that deviated the entire visual field 10° to the right (Rossetti et al. 1998; Redding et al. 2005; Rode et al. 2006; Pisella et al. 2006; Jacquin-Courtois et al. 2013; Crottaz-Herbette et al. 2014). The aftereffect was assessed immediately after the adaptation by measuring the pointing errors. Subjects fixated a dot without prisms, then closed their eyes and pointed to the dot. The pointing error was measured twice, for the left and the right dot. Negative values corresponded to a deviation of the pointings to the left of the targets. The pointing errors to both dots were averaged and compared across experimental groups using an unpaired *t* test.

### Imaging data acquisition

MRI and event-related fMRI were acquired at the Lemanic Biomedical Imaging Center (CIBM) in the CHUV, Lausanne on a 3T Siemens Prisma scanner (auditory task) with a standard 20-channel head-coil and on a 3T Siemens Trio scanner (visual task) with a standard 32-channel head-coil. Functional MR images were acquired with a single-shot echo planar imaging gradient echo sequence (repetition time = 2 s; flip angle = 90°; echo time = 30 ms; number of slices = 32; voxel size = 2 × 2 × 3 mm (auditory task), 3 × 3 × 3 mm (visual task); 10% gap). The 32 slices, were acquired in a sequential ascending order, and covered the whole head volume in the AC-PC plane. A high-resolution T1-weighted 3D gradient echo sequence was acquired for each participant (240 slices (auditory task), 160 slices (visual task), voxel size = 1 × 1 × 1 mm). These T1 images were used for the co-registration with the functional images in the subsequent processing procedure.

### Data analysis

#### Behavioral tasks

On behavioral data acquired during fMRI, mixed three-way ANOVAs were conducted on the mean accuracy and on the mean reaction times with Modality (auditory, visual) as a between-subjects factor; and Session (pre, post) and

Stimulus position (left, center, right) as within-subject factors. Analyses were processed using R (R Development Core Team 2008, Vienna, Austria).

### fMRI data

Auditory and visual imaging data were processed using Statistical Parametric Mapping (SPM12, Wellcome Department of Cognitive Neurology, London, UK). Data were first corrected for motion by applying a six-parameter rigid-body transformation minimizing the difference between each image and the first scan. Slice timing correction was performed on these realigned images. For each participant, these functional images and the anatomical image were co-registered and then normalized to the Montreal Neurological Institute (MNI) template using the deformation field calculated by SPM12. Normalized functional images were resliced to a  $2 \times 2 \times 2$  mm voxel size and anatomical images to a  $1 \times 1 \times 1$  mm voxel size. These functional images were finally spatially smoothed to increase the signal-to-noise ratio using an isotropic Gaussian kernel of 6 mm FWHM. Statistics at the subject-level were done across the whole brain in a voxelwise manner. The general linear model was conducted using a canonical hemodynamic response. The six realignment parameters were included in the model as regressors. Linear contrasts were specified for the two sessions in the same design matrix.

In the second-level analysis, a mixed-design ANOVA was performed with the factor Modality (auditory, visual) as a between-subject factor and the factor Stimulus position (left, center, right) and Session (pre, post) as within-subject factors. From this ANOVA, the main effect of the factor Session allowed determining which regions are modulated by R-PA independently of the Modality or Stimulus position. The interaction between the factor Session and Stimulus position revealed where R-PA's effect varies with the change in stimulus position independently of the modality. Post hoc

ANOVAs on the factor Stimulus position and Session were conducted separately for each modality. The statistical maps of activation for these analyses were thresholded at  $p < 0.05$  and cluster extent of  $k = 50$  (above the expected number of voxels per cluster as provided automatically by SPM12). The interaction between the factor Modality and Session revealed where the effect of R-PA is different between modalities, independently of the stimulus position. The statistical maps of activation for this analysis were thresholded at  $p < 0.05$  and cluster extent of  $k = 36$  (above the expected number of voxels per cluster as provided automatically by SPM12).

### Regions of interest

The regions of interest (ROIs) analyses were conducted on the clusters of activation in the IPL in the interaction between the factor Stimulus position and Session. They were constructed as spheres with a 3 mm diameter.

## Results

### Behavioral data

The visuo-motor R-PA aftereffect, i.e., the pointing error after the removal of the prisms, was observed in the group performing the auditory ( $M = -7.12^\circ$ ,  $SD = 1.4^\circ$ ) and the visual paradigm ( $M = -8.6^\circ$ ,  $SD = 2.6^\circ$ ) and did not differ significantly between the groups,  $t(23.5) = 1.96$ ,  $p = 0.06$ .

The accuracy and reaction times of the visual and of the auditory detection tasks performed during the fMRI paradigm were analyzed using mixed-design ANOVAs with the factor Modality (auditory, visual) as a between-subjects factor and the factors Stimulus position (left, center, right) and Session (pre, post) as within-subject factors (Table 1). Subjects showed high accuracy for all conditions, ranging between 90 and 100%. The ANOVA on accuracy data

**Table 1** Behavioral results for the detection tasks. Mean and standard deviation (SD) for the accuracy and the reaction time (RT), by Session and Stimulus position

Pre					Post				
	Left	Center	Right	Mean		Left	Center	Right	Mean
Auditory					Auditory				
Mean RT (ms)	403.0	411.0	411.0	408.3	Mean RT (ms)	391.0	383.0	400.0	391.3
SD of RT	105.3	100.7	95.3	100.5	SD of RT	101.5	107.5	105.9	105.0
Mean accuracy (%)	98.9	97.5	99.3	98.6	Mean accuracy (%)	98.6	98.6	99.6	98.9
SD of accuracy	2.1	4.3	2.7	3.0	SD of accuracy	3.06	2.34	1.3	2.3
Visual					Visual				
Mean RT (ms)	408.0	400.0	405.0	404.3	Mean RT (ms)	424.0	409.0	420.0	417.7
SD of RT	54.8	53.3	49.3	52.5	SD of RT	71.2	55.4	56.4	61.0
Mean accuracy (%)	97.9	100.0	96.8	98.2	Mean accuracy (%)	99.3	98.9	99.6	99.3
SD of accuracy	3.8	0.0	6.1	3.3	SD of accuracy	1.8	2.9	1.3	20.0

showed a significant interaction between the factor Modality and Stimulus position [ $F(2, 52) = 4.202, p = 0.02$ ], which was driven by a lower accuracy for right targets in the visual modality and for central targets in the auditory modality. The other interactions and all main effects were not significant.

For the reaction times, the ANOVA showed a significant main effect of the factor Stimulus position [ $F(2, 26) = 3.25, p = 0.047$ ], subjects had shorter reaction times for central stimuli and longer reaction times for right stimuli. Results also showed a significant interaction between the factor Session and Modality [ $F(2, 52) = 4.609, p = 0.041$ ]. This interaction was driven by longer reaction times after R-PA compared to before R-PA in the visual task, and vice-versa for the auditory task.

In summary, behavioral results confirmed that the tasks at hand were fit for the use of a spatiotopic analysis. First, both the auditory and the visual detection tasks were performed at a high level of accuracy, which was not modulated by R-PA. Second, although reaction times were modulated by R-PA, the effect did not differ in a given modality between the three positions.

### Intervention-related changes in activation patterns

Activation patterns elicited by the target detection tasks were analyzed by a general mixed-design ANOVA including the between-subject factor Modality (auditory, visual) and the within-subject factor Stimulus position (left, center, right) and Session (pre, post). The following analyses addressed our specific hypotheses.

#### General impact of R-PA on spatial processing

The main effects of the factor Session (Fig. 1a) involved a large activation in the left angular gyrus and, to smaller extents, bilateral activations in the insula, supramarginal gyrus, superior temporal gyrus, and prefrontal regions; left activations in the cerebellum and right activations in the middle temporal gyrus and the precuneus. These effects did not depend on the modality or on the stimulus position.

#### Modulation of the representation of the ipsilateral space within IPL

The interaction between the factor Stimulus position and Session, independently of the modality, was significant in the left and right IPL, the left Heschl's gyrus, the right fusiform gyrus and to a smaller extent, in the middle frontal gyrus, precuneus and insula on both hemispheres (Fig. 1b; Table 2 for more details). ROIs analyses (Fig. 1c; Table 2) showed that within the left and right IPL, this interaction was driven by an increase in activation after R-PA when targets were on the left and center and a decrease in activation after R-PA

when targets were on the right. Thus, R-PA induced greater activation for ipsilateral targets within the left hemisphere and a decrease in activation for ipsilateral targets in the right IPL, independently of the target modality.

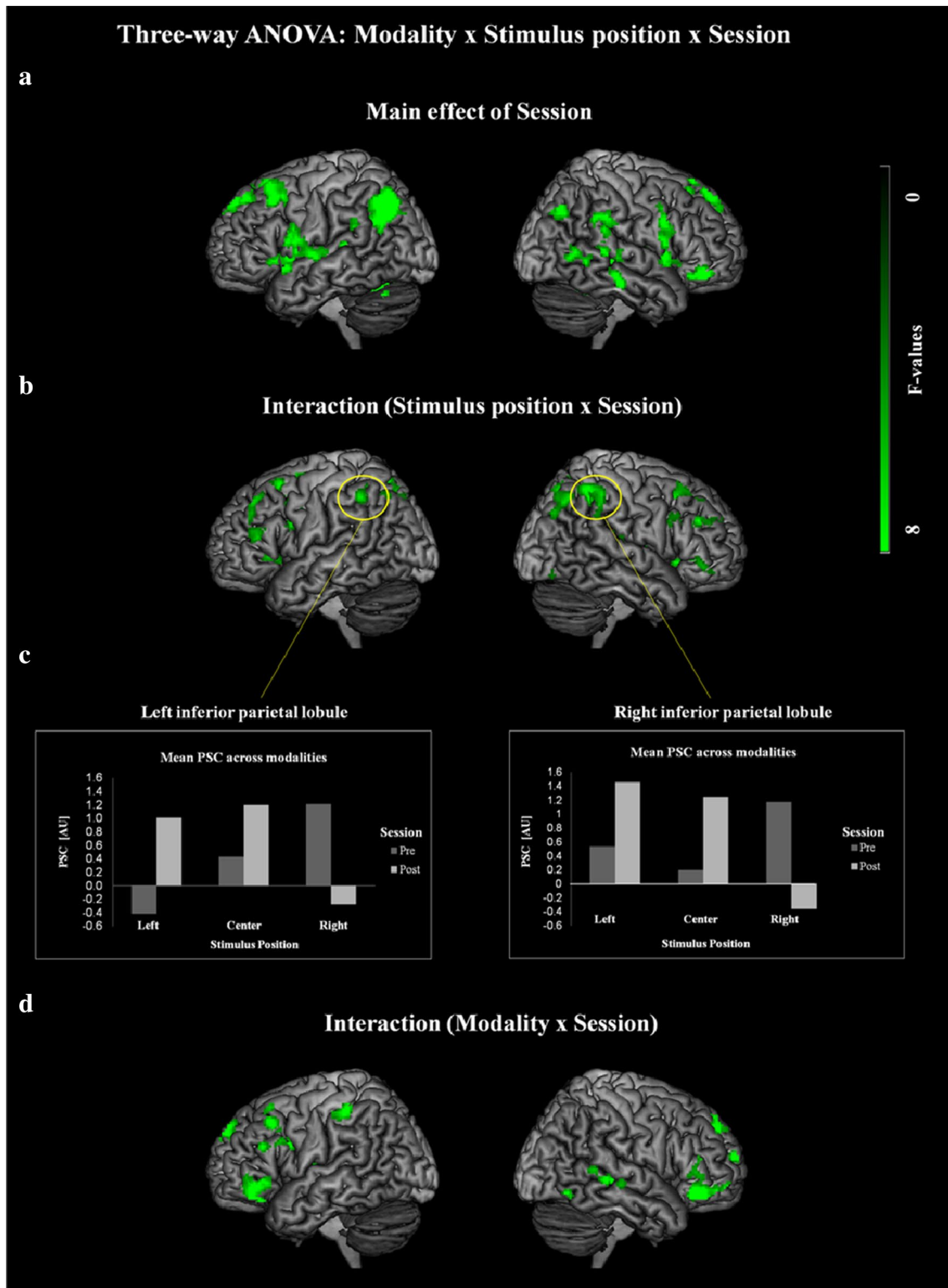
#### Modality-specific effects of R-PA

Putative differences in the effect of R-PA on either modality were assessed by the interaction Modality  $\times$  Session. No significant interaction was present in IPL on either side. Small significant clusters were observed in the left postcentral gyrus, insula and cerebellum, in the right middle temporal sulcus and bilaterally in the middle and inferior frontal gyri (Fig. 1d).

The modality-specific effect of R-PA was assessed for each modality with two-way ANOVAs including the within-subject factor Stimulus position (left, center, right) and Session (pre, post). In the left IPL, more precisely in the angular gyrus, the cluster showing a significant main effect of Session for the auditory modality overlapped with the cluster showing a significant main effect of Session for the visual modality (Fig. 2top, Table 3). In the right hemisphere, auditory and visual tasks also led to a main effect of Session in the IPL, but in the supramarginal gyrus. These activations in the right SMG in each modality were adjacent, not overlapping. In addition to the angular and supramarginal gyri, significant main effect of Session included in the auditory modality bilaterally prefrontal regions, the cerebellum, the precuneus and superior temporal gyri; the left inferior parietal lobule and postcentral gyrus and the right middle temporal gyrus; and in the visual modality bilaterally prefrontal regions, and the right middle temporal gyrus (Fig. 2top, Table 3).

The effect of R-PA on spatial representations in each modality was assessed in ROIs centered on peaks of activation in the IPL (for coordinates see Table 3). In the auditory modality, the increased activity observed on the left hemisphere and the decreased activity observed on the right hemisphere corresponded respectively to the enhancement of the representation of the left, central and right space within the left angular gyrus and to the decreased representation of the right space (and partially of the central and left space) in the right supramarginal gyrus (Fig. 2bottom part). Similarly, in the visual modality, the representation of the left, central and right space was enhanced within the left angular gyrus, whereas the representation of the right space decreased in the right supramarginal gyrus.

Post hoc analyses ( $t$  tests) on the activation related to the effect of R-PA on each stimulus position and on each modality separately confirmed these changes (Supplementary Information). In particular, surface renderings of the activation showed that R-PA yielded a significant increase in the representation of the left, central and right space within



**Fig. 1** Surface renderings of significant brain activations during the auditory and visual detection tasks in the mixed-design ANOVA, for **a** the main effect of Session, **b** the interaction Stimulus position  $\times$  Session and **d** the interaction Modality  $\times$  Session. **c** Barplots

illustrating the percent signal changes (PSC) for the left (coordinates:  $-48/-46/46$ ) and right IPL (coordinates:  $-42/-50/52$ ) for both tasks at each stimulus position. All maps are thresholded at  $p < 0.05$ ,  $k = 50$

**Table 2** Coordinates of the main clusters, listed in MNI atlas space with their local maxima and anatomical details of their extend, showing significant effects for the interaction (Stimulus position  $\times$  Session) in the general ANOVA

Anatomical region	H	BA	MNI coordinates	Peak intensity	Nb of voxels
Interaction (Stimulus position $\times$ Session)					
Inferior parietal lobule, supramarginal gyrus	R	40	42/–50/52	8.83	501
Inferior parietal lobule	L	40	–48/–46/46	7.35	204
Middle frontal gyrus, superior frontal gyrus	R	8/9	32/18/46	7.33	135
Fusiform gyrus, lingual gyrus and middle occipital gyrus	R	37/18/19	32/–66/–12	5.51	152
Fusiform gyrus, parahippocampal gyrus	L	37	–36/–50/–16	5.83	50
Inferior frontal gyrus, middle frontal gyrus	L	45/46	–40/30/20	7.97	138
Insula, inferior frontal gyrus	R	13/14/47/45	36/20–4	7.44	104
Insula, inferior frontal gyrus	L	13/14/45/47	–38/22/0	6.63	129
Precuneus, superior and inferior parietal lobules, cuneus, superior occipital lobe	L	7/5/40/17	–6/–72/46	8.31	789
Precuneus, superior and inferior parietal lobules, angular gyrus, superior occipital lobe	R	7/5/40/39/17	4/–64/54	7.93	805
Hippocampus	R		28/–8/–20	12.55	76

the left IPL and a significant decrease of right space in the right IPL for the auditory modality. For the visual modality surface renderings of R-PA-related activation showed that R-PA yielded a significant increase in the representation of the left, central and right space within the left IPL and a significant decrease of right auditory space in the right IPL.

In summary, these results demonstrate that R-PA modulates within the right and left IPL not only visuo-spatial but also auditory spatial representations. Furthermore, they provide the following answers to our hypotheses. First, R-PA has an impact on visual and auditory attentional processing within the left and right IPL, as demonstrated by a massive main effect of Session, independently of the modality. Second, the significant interaction between the factor Stimulus position and Session, independently of the modality, confirmed that R-PA enhances the representation of the ipsilateral space within the left IPL and decreases it within the right IPL. Third, the modulation by R-PA within the IPL did not differ between the modalities, as indicated by the lack of significant interaction in the IPL between the factor Modality and Session. Fourth, R-PA-modulated spatial representations within the IPL in either modality, as demonstrated by modality-specific ANOVA analysis. In particular, in either modality, the representation of the left, central and right space increased in the left IPL, whereas the representation of the right space decreased in the right IPL.

## Discussion

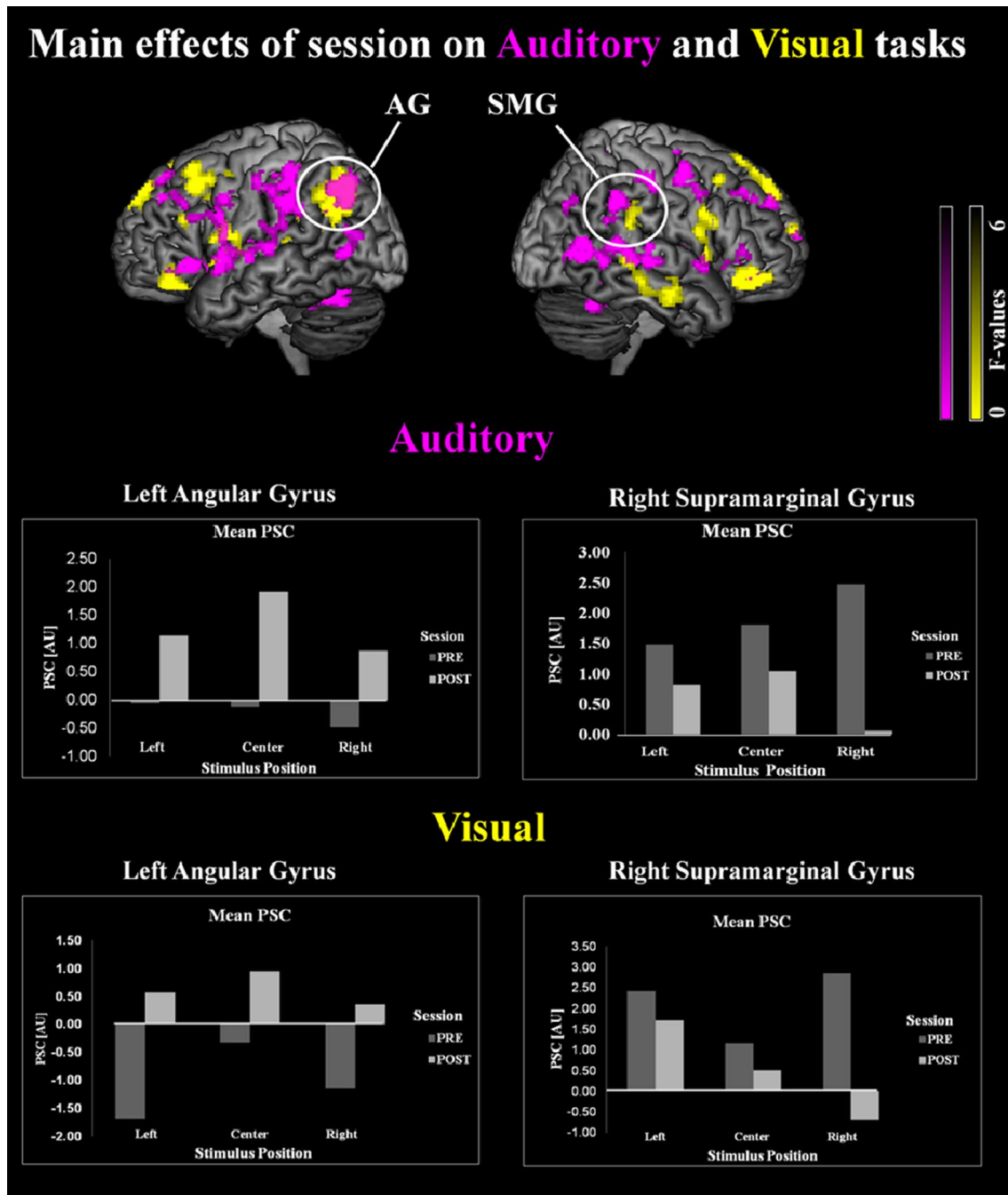
Our results demonstrate that a brief exposure to R-PA modulates the processing of auditory stimuli within the inferior parietal cortex. It enhances the involvement of the left angular gyrus in the detection of left, central and right targets and

decreases the involvement of the right supramarginal gyrus for right targets. Thus, R-PA shifts hemispheric dominance for auditory spatial attention from the right to the left IPL. This effect of R-PA is similar to the previously described hemispheric shift for visuo-spatial attention (Crottaz-Herbette et al. 2014; Clarke and Crottaz-Herbette 2016).

The above described changes occur very rapidly, following a brief exposure to R-PA. The underlying neural mechanisms may, therefore, rely on pre-existing ipsilateral representations of the auditory space within the left hemisphere and on supramodal effects of PA. Furthermore, the R-PA-induced shift in hemispheric dominance for auditory spatial attention offers a parsimonious explanation for the previously reported effects on dichotic listening (Jacquin-Courtois et al. 2010; Tissieres et al. 2017) and auditory target detection in neglect (Eramudugolla et al. 2010).

## Networks underlying auditory spatial representations and auditory attention

Studies in non-human primates indicate that auditory areas encode auditory space in a distributed fashion, without an orderly topographical map (Stecker et al. 2003, 2005; Harrington et al. 2008). Single neurons tend to have large receptive fields which are centered on locations within the contralateral space (Recanzone 2000; Stecker et al. 2003; Woods et al. 2006). Human auditory areas on the supratemporal plane are organized very similarly, but with hemispheric differences. fMRI studies reported preferential responses to contralateral locations with broad spatial tuning (Derey et al. 2016; McLaughlin et al. 2016). Activation patterns revealed greater bilaterality of responses on the right and stricter contralaterality on the left supratemporal side (Stecker et al. 2015).



**Fig. 2** Surface renderings of brain activations for the main effect of Session during the auditory and visual tasks separately (in the two-way ANOVA Stimulus position  $\times$  Session). Activations for the auditory task in purple and for the visual task in yellow. Barplots illustrating

the percent signal changes (PSC) in the left AG and right SMG for each task at each stimulus position. All maps are thresholded at  $p < 0.05$ ,  $k = 36$

The representation of the auditory space outside the supratemporal plane is largely asymmetrical, with a right-hemispheric dominance. A series of fMRI (Bushara et al. 1999; Maeder et al. 2001; Arnott et al. 2004; De Santis et al. 2007), magnetoencephalography (Kaiser et al. 2000), transcranial magnetic stimulation (At et al. 2011; Lewald

and Getzmann 2011) and lesion studies (Spierer et al. 2009) reported the involvement of the right fronto-parietal cortex in the representation of the whole auditory space, whereas the left fronto-parietal cortex was focused on the contralateral, right space. Comparing activation patterns elicited by auditory stimuli in left, central or right failed to



**Table 3** Main effect of Session for each Modality separately. Coordinates of the main clusters, listed in MNI atlas space with their local maxima and anatomical details of their extent, showing significant activation for the main effect of Session on the two-way ANOVAs

Anatomical region	H	BA	MNI coordinates	Peak intensity	Nb of voxels
<b>Auditory task</b>					
Angular gyrus: cluster extending to inferior parietal lobule, superior parietal lobule, precuneus	L	39/40/7	−44/−60/40	11.39	516
Angular gyrus	R	39	48/−74/32	7.47	36
Supramarginal gyrus: cluster extending to inferior parietal lobule	R	40	58/−42/34	13.45	179
Supramarginal gyrus: cluster extending to postcentral gyrus, superior temporal gyrus and inferior temporal gyrus	L	40/38/5	−62/−32/34	15.02	727
<b>Visual task</b>					
Angular gyrus: cluster extending to inferior parietal lobule, supramarginal gyrus, middle and superior temporal gyri	L	39/40/42	−44/−62/30	18.82	788
Supramarginal gyrus: cluster extending to inferior parietal lobule, superior temporal gyrus	R	40/42/21	60/−32/28	7.75	127

reveal topographic representations of the auditory space; however, stronger activation were reported by central auditory stimuli in the right IPL and by left stimuli in the posterior part of the left middle temporal gyrus (Zimmer et al. 2006).

Electrophysiological studies suggest two stages of auditory spatial processing; at short post-stimulus latencies, each hemisphere appears to involve preferentially the contralateral temporoparietal cortex, while at latter latencies both hemispheres implicate the right parietal cortex, reflecting the right-hemispheric dominance for auditory spatial representation (Kaiser and Lutzenberger 2001; Tardif et al. 2006; De Santis et al. 2007; Spierer et al. 2009; At et al. 2011). Patterns of structural and functional connectivity further support this fronto-parietal asymmetry and the right-hemispheric dominance model for auditory spatial perception (Dietz et al. 2014; Cammoun et al. 2015).

Auditory spatial representations are malleable and can be modulated by auditory manipulations. In a behavioral study, subjects were exposed to long-term monaural distortions of the perceived spectrum, which lead to deficits in sound localization with subsequent recalibration of the percept (Wanrooij and Opstal 2005). A later imaging study demonstrated that behavioral recalibration due to shifted interaural time differences was associated with shifts of spatial representation within both hemispheres (Trapeau and Schönwiesner 2015).

The simultaneous presentation of auditory and visual stimuli at different locations can introduce a bias to the auditory spatial perception. Referred to as the ventriloquism effect, this phenomenon appears rapidly and can last for over 20 min (Recanzone 1998). EEG and fMRI studies reported changes in auditory spatial representations and highlighted the role of the left–right balance within the planum temporale as putative neural mechanism (Bonath et al. 2007, 2014).

The effect of R-PA is not the only example of supramodal effect of visuo-motor adaptation on auditory spatial functions. A previous behavioral study reported the effects of a visuo-motor adaptation through exposure to a rotated screen cursor–hand relationship. A brief exposure yielded visuo-motor and similar auditory-motor after effects. This adaptation effect did not require active cross-modal experience (Kagerer and Contreras-Vidal 2009).

Attending to auditory stimuli involves a wide range of regions in either hemisphere. Non-spatial auditory alertness was shown to rely on an extended, predominantly right-hemispheric network including frontal, cingular, inferior parietal, temporal and thalamic regions (Sturm et al. 2004). Comparing regions involved in auditory and in visual alertness revealed modality-specific regions within posterior parietal and frontal cortices; the only region involved in both modalities was the right superior temporal gyrus (Thiel and Fink 2007).

Auditory spatial attention was investigated with different paradigms, which highlighted the contribution of different neural networks. Selective attention to stimuli presented in one ear was found to activate the supplementary motor area, the left postcentral cortex and precentral regions bilaterally; in addition the superior temporal gyrus was activated, with a preference for attending to the contralateral ear (Tzourio et al. 1997; Alho et al. 1999). A later study reported an overall right-hemispheric dominance for auditory attention, which was modulated by eye position (Petit et al. 2007).

Selective attention to auditory or visual stimuli, which were presented in simultaneous streams, activated, in addition to the modality-specific cortices, overlapping regions in the inferior parietal cortex, more on the right than the left side (Salo et al. 2013). Smith and colleagues (Smith et al. 2010), with an orthogonal-cueing paradigm, investigated in a within-subject design the similarities between the patterns of activations for visual and auditory stimuli during a

spatial attentional task. Results showed that visual and auditory tasks recruit similar networks. The regions common to the two spatial tasks highlighted by their study are the supplementary motor area, the posterior parietal cortex and the frontal eye fields. The authors suggest that these three areas might be representative of a supramodal attentional network.

In summary, the above-quoted evidence shows that representation of the auditory space and auditory attention depends to a great extent on a right-dominant parieto-frontal network. There are, however, indications that the left hemisphere may comprise discrete representations of the ipsilateral auditory space. An fMRI study reported that the left middle temporal gyrus, but not the IPL was strongly activated by left-sided auditory stimuli (Zimmer et al. 2006). A later EEG study has shown that a left temporo-prefrontal network supported a position-linked representation of sound objects across the whole auditory space (Bourquin et al. 2013; Clarke and Geiser 2015). It is currently unclear, how far these left-hemispheric representations contribute to the effect of R-PA. Alternatively, the left-lateralized motor attentional system (Rushworth et al. 2001, 2003) may be at the origin of the bilateral spatial representation within the left IPL.

The supramodal effect of R-PA on auditory space representation is in line with the previously described examples of auditory–visual spatial interactions, such as the ventriloquism effect (e.g., Bonath et al. 2014, 2007; Recanzone 1998) or auditory-motor after effects following visuo-motor adaptation (Kagerer and Contreras-Vidal 2009).

### Auditory neglect and rightward prismatic adaptation

Auditory neglect is characterized by impaired attention to left-sided stimuli. Most commonly, this is observed in paradigms where auditory stimuli are presented from the right and left side simultaneously, to either ear (dichotic listening: Heilman and Valenstein 1972; Hugdahl et al. 1991) or lateralized to the left or right space by means of interaural cues (diotic listening: Bellmann et al. 2001; Thiran and Clarke 2003; Spierer et al. 2007). Neglect phenomena have been also proposed to play a role in alloacousia, i.e., systematic left to right bias in sound localization (Bisiach et al. 1984). Left-sided extinction on dichotic or diotic listening and the distortion of auditory space perception can occur independently of each other and define most likely different types of auditory neglect (Bellmann et al. 2001; Thiran and Clarke 2003; Spierer et al. 2007).

Two previous studies demonstrated an effect of R-PA on auditory neglect. In both instances, the shift in hemispheric dominance for auditory spatial attention from the right to the left IPL, which we have described here, offers a parsimonious explanation of the underlying neural mechanisms.

The ventral attentional system is known to be involved in the detection of unexpected stimuli, and therefore, in the reorienting of attention (Corbetta and Shulman 2002; Igelström and Graziano 2017; Shulman et al. 2003, 2010; Todd et al. 2005). In neglect, it is generally damaged and can no longer support the detection of targets (Corbetta and Shulman 2002). The shift of the ventral attentional system to left IPL is likely to restore the alerting input to the dorsal attentional system on either sides, both for auditory and visual targets (Crottaz-Herbette et al. 2014, 2017a; Clarke and Crottaz-Herbette 2016).

In the first study, R-PA was shown to improve overall performance on auditory target detection without, however, restoring the spatial gradient of attention (Eramudugolla et al. 2010). The overall improvement may be related to our observation that R-PA enhances left IPL activation by auditory stimuli independently of whether they occur in left, central or right space. Two other studies demonstrated R-PA-induced alleviation of left ear extinction on dichotic listening; this effect was specific to the detection asymmetry between the two ears and did not affect general arousal (Jacquin-Courtois et al. 2010; Tissieres et al. 2017). The side-specific effect in this study may be due to the nature of stimuli which were used. Both studies used a verbal dichotic listening paradigm, in which pairs of phonological similar bisyllabic words were presented and the task consisted in repeating the words. The repetition task depends critically on left-hemispheric speech networks. It is likely that the restoration of the left ear input to the left IPL had in this configuration a greater functional impact than the enhancement of the right ear input.

### Direction-specific effects of PA

Several lines of evidence suggest that partially different neural mechanisms underlie the effects of R-PA and L-PA. R-PA was shown to induce a shift in hemispheric dominance of the ventral attentional system from the right to the left hemisphere in the visual modality, both in normal subjects and in neglect patients (Crottaz-Herbette et al. 2014, 2017a), and in the auditory modality (here). This shift offers a parsimonious explanation of behavioral effects of R-PA. In normal subjects, only few such changes were reported and they can be attributed to the changes in information flow between early-stage visual areas and the right and left IPL (for detailed discussion see (Clarke and Crottaz-Herbette 2016): (1) the rightward shift in visual midpoint judgments in extrapersonal, but not in peripersonal space (Berberovic and Mattingley 2003); speeding of exogenous reorienting of attention from invalid cues for targets on the right side (Striener et al. 2006); and (2) the modulation of oculomotor performance in a double-step saccade paradigm (Bultitude et al. 2013). In neglect, R-PA was reported to reduce the

visuo-spatial bias in tasks which involve the dorsal attentional system (Striemer and Danckert 2010); this effect is likely to be mediated by the left IPL, which after R-PA relays stimulus-driven input to the right dorsal attentional system (for detailed discussion see Clarke and Crottaz-Herbette 2016). R-PA was also found to alleviate left ear extinction in dichotic listening tasks (Jacquin-Courtois et al. 2010; Tisseries et al. 2017). The shift of left auditory space representation to the left IPL offers a likely explanation for this effect.

L-PA was shown to strengthen right-hemispheric dominance of the ventral attentional system by enhancing the representation of the right visual space within the right IPL (Crottaz-Herbette et al. 2017b). The resulting overemphasis of the right visual space within the right IPL offers a parsimonious explanation of neglect-like effects induced by L-PA in normal subject performances (Colent et al. 2000; Martín-Arévalo et al. 2016; Crottaz-Herbette et al. 2017b).

## Conclusions

A brief exposure to R-PA modulated the representation of the auditory and of the visual space within the ventral attentional system by enhancing, in either modality, the representation of the left, central and right space in the left IPL, and reducing the representation of the right space in the right IPL. The effect of R-PA occurred very rapidly and may, therefore, rely on pre-existing ipsilateral spatial representations within the left hemisphere. Previous studies suggest that discrete parts of the left hemisphere may encode ipsilateral auditory space. The left middle temporal gyrus, but not the IPL, was reported to be strongly activated by left-sided auditory stimuli (Zimmer et al. 2006). A left temporo-frontal network was shown to support a position-linked representation of sound objects across the whole auditory space (Bourquin et al. 2013; Clarke and Geiser 2015). Alternatively, the bilateral spatial representations within the left IPL may be related to the left-lateralized motor attentional system (Rushworth et al. 2001, 2003).

The modulation of auditory spatial representations by R-PA is a further example of auditory–visual interactions, such as those involved in the ventriloquism effect (e.g., Bonath et al. 2014, 2007; Recanzone 1998) or auditory–motor after effects following visuo–motor adaptation (Kagerer and Contreras-Vidal 2009).

The shift in hemispheric dominance for auditory spatial attention from the right to the left IPL offers a parsimonious explanation for the effect of R-PA on dichotic listening and target detection in neglect (Jacquin-Courtois et al. 2010; Eramudugolla et al. 2010). It is currently unknown, whether R-PA affects similarly other auditory symptoms of neglect, such as the shift in auditory spatial attention and alloacousia.

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## Compliance with ethical standards

**Conflict of interest** The authors reported no conflict of interest.

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