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A network view on brain regions involved in experts' object and pattern recognition: Implications for the neural mechanisms of skilled visual perception

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Abstract

Skilled visual object and pattern recognition form the basis of many everyday behaviours. The game of chess has often been used as a model case for studying how long-term experience aides in perceiving objects and their spatio-functional interrelations. Earlier research revealed two brain regions, posterior middle temporal gyrus (pMTG) and collateral sulcus (CoS), to be linked to chess experts' superior object and pattern recognition, respectively. Here we elucidated the brain networks these two expertise-related regions are embedded in, employing resting-state functional connectivity analysis and meta-analytic connectivity modeling with the BrainMap database. pMTG was preferentially connected with dorsal visual stream areas and a parieto-prefrontal network for action planning, while CoS was preferentially connected with posterior medial cortex and hippocampus, linked to scene perception, perspective-taking and navigation. Functional profiling using BrainMap meta-data revealed that pMTG was linked to semantic processing as well as inhibition and attention, while CoS was linked to face and shape perception as well as passive viewing. Our findings suggest that pMTG subserves skilled object recognition by mediating the link between object identity and object affordances, while CoS subserves skilled pattern recognition by linking the position of individual objects with typical spatio-functional layouts of their environment stored in memory.

Keywords: skilled perception; chess expertise; functional connectivity; resting-state fMRI; MACM; functional decoding

1. Introduction

In everyday life, we are often surrounded by highly familiar objects, which are usually placed in particular spatial contexts and associated with particular functions. Through repeated experience, we learn these associations. As a result, skilled visual perception does not only comprise the efficient and seemingly effortless recognition of a given object per se but also of its spatial and functional relations to other objects and potential ways of putting the object to use. When objects can be manipulated (e.g., moved), this familiarity includes typical actions (e.g., movement trajectories) to meet particular ends. To further the understanding of how these individual processes come together and are mediated by the brain, we used the game of chess as a well-controlled but ecologically valid model case for the skilled visual perception of movable objects embedded in complex relationships.

Using chess as a model case has a long tradition in cognitive psychology and neuroscience research (Amidzic, Riehle, Fehr, Wienbruch, & Elbert, 2001; Bilalić, 2017; Bilalić, 2016; Boggan, Bartlett, & Krawczyk, 2012; Charness, 1992; Chase & Simon, 1973). On the one hand, chess offers a complex and rich environment that requires a broad range of cognitive operations; on the other, it uses simple objects and rules that clearly specify and constrain the environment. Therefore, one can examine higher cognitive processes such as problem solving (Bilalić, McLeod, & Gobet, 2008, 2009; Connors, Burns, & Campitelli, 2011) and decision making (Bilalić & McLeod, 2014; Merim Bilalić, McLeod, & Gobet, 2008b, 2008a) as well as more basic perceptual processes such as object or pattern recognition (Gobet & Simon, 1996; Kiesel, Kunde, Pohl, Berner, & Hoffmann, 2009; Saariluoma, 1990). In this paper we will focus on the neural mechanisms behind skilled object and pattern recognition at the brain network level.

Chess positions consist of individual objects, chess pieces, with characteristic shapes that need to be recognized by the player. This object recognition, in turn, allows ascribing functions to

individual objects, based on the rules of their movement. That is, object recognition leads, via rule retrieval from long-term memory, to options for moving a given object on the board. Put differently, recognizing a particular chess piece is tightly connected with activating the representation of potential actions upon this piece. However, beyond object identification, it is the relations between objects that are essential for understanding the gist of a given game situation. This is because realistic movement options for a given object, out of the theoretically possible range as defined by an object's identity, depend on the location of that object, relative to board borders and other objects. Recognizing the spatial pattern of interdependencies between objects is pivotal for grasping the entire position and choosing the optimal move. It has also been shown that recognizing the relationship between pairs of potentially interacting objects also helps in recognizing the objects themselves (Roberts & Humphreys, 2010, 2011). Therefore, recognizing an opposing chess piece and its potential movements will facilitate recognizing one's own pieces that are potentially under threat (i.e., objects targeted by the potential actions of the opposing object).

It is known that chess experts have superior domain-specific object recognition abilities, as compared with novices (Ericsson & Lehmann, 1996; Ericsson & Charness, 1994), even in simple paradigms where single isolated chess pieces are to be recognized (Kiesel et al., 2009; Saariluoma, 1990). The expertise advantage is particularly pronounced, however, when there are numerous objects (Reingold, Charness, Pomplun, & Stampe, 2001; Reingold, Charness, Schultetus, & Stampe, 2001; Saariluoma, 1995). As alluded to above, this is because identifying a particular object among several others not only requires object recognition skills but also benefits from knowledge about typical locations and relations between objects in the domain-specific environment (Chase & Simon, 1973; Gobet & Simon, 1996).

In a series of studies (Bilalić, Kiesel, Pohl, Erb, & Grodd, 2011; Bilalić, Langner, Erb, & Grodd, 2010; Bilalić, Turella, Campitelli, Erb, & Grodd, 2012; Bilalić, Langner, Ulrich, & Grodd,

2011; Rennig, Bilalić, Huberle, Karnath, & Himmelbach, 2013), we have tackled the question of the neural mechanisms behind skilled object and pattern recognition in chess, focusing on differences in regional brain activity between experts and novices. These studies localized two brain areas specifically involved in experts' superior object or pattern recognition, respectively: posterior middle temporal gyrus (pMTG) and collateral sulcus (CoS; Bilalić, Kiesel, et al., 2011; Bilalić et al., 2010, 2012). However, complex cognitive functions are not brought about by the isolated activity of single brain regions but rather by interactions between different regions that form nodes of a network. An important step toward understanding the neural mechanisms of expert performance is, therefore, to delineate the functional neural networks in which expertise-related regions are embedded. To this end, we combined seed-based resting-state functional connectivity (RSFC) analysis with meta-analytic connectivity modelling (MACM).

RSFC analysis allows the identification of functional brain networks while participants are at rest, that is, during unconstrained cognition (Buckner, Andrews-Hanna, & Schacter, 2008; Smith et al., 2009). MACM, in turn, uses information on a given region's activity across all kinds of tasks stored in databases like BrainMap (www.brainmap.org) to identify other brain regions that are consistently co-activated with the given region (Eickhoff et al., 2011; Fox, Lancaster, Laird, & Eickhoff, 2014). Combining both approaches then yields brain regions that are functionally connected with a given seed region across both task-free and task-constrained states, strengthening the validity of the findings.

For the pMTG, involved in skilled object recognition, we hypothesized enhanced functional connectivity (FC), relative to the CoS, with higher-order visual areas of the ventral stream such as the lateral occipital complex, which is known to subserve stimulus shape identification (Grill-Spector, Kourtzi, & Kanwisher, 2001; Pourtois, Schwartz, Spiridon, Martuzzi, & Vuilleumier, 2008). As object recognition in chess also entails realising potential moves of the recognized piece,

we also expected that the pMTG showed preferential FC with regions involved in movement detection (visual area V5; Beckers & Zeki, 1995), spatial cognition (intraparietal sulcus and superior parietal cortex; de Rover et al., 2008; Kravitz, Saleem, Baker, & Mishkin, 2011), cognitive action control (premotor cortex, inferior frontal junction; Brass, Derrfuss, Forstmann, & von Cramon, 2005; Chouinard & Paus, 2006; Langner et al., 2014) and action planning (supramarginal gyrus; Canessa et al., 2008; Kellenbach, Brett, & Patterson, 2003). Finally, we expected the FC pattern to be different for left and right pMTG seeds, as our previous studies have shown that experts engage both left and right pMTG, while novices use only the left pMTG. This phenomenon of the bilateral engagement in experts is also found in other domains and has been the named the "double take of expertise" (Bilalić, 2017; Bilalić, Kiesel, et al., 2011; Bilalić et al., 2012).

As for the CoS, involved in skilled pattern recognition, we hypothesized enhanced FC, relative to pMTG, with areas of the ventral visual stream linked to scene recognition/reconstruction, such as the retrosplenial cortex/ventral posterior cingulate cortex (Epstein, 2008; Epstein, Harris, Stanley, & Kanwisher, 1999). As our previous studies did not reveal significant laterality effects associated with experts' pattern recognition, we did not expect strongly lateralized CoS FC patterns. As mentioned above, both skilled object and pattern recognition in chess have a strong spatial component: experts use their knowledge on typical object locations and spatial relations between objects for identifying both individual objects and entire object configurations, and their identification of chess pieces involves the immediate recognition of potential move (i.e. action) trajectories in space. As a common neural substrate, we therefore expected shared FC of both pMTG and CoS not only with areas of the ventral visual stream, related to object identification, but also with the dorsal visual stream, involved in spatial aspects of vision and visually guided action (Goodale & Milner, 1992, 2018; Mishkin, Ungerleider, & Macko, 1983; Ungerleider & Haxby, 1994).

In a final step, we capitalized on the meta-data stored in the aforementioned BrainMap database, which provide information on behavioural domains and paradigm classes associated with stored activation coordinates. We used these meta-data to characterize the functional roles of our regions of interest by means of meta-analytic quantitative forward inference. This provided us with objective information on the cognitive functions of our seed regions synthesized across many neuroimaging experiments, beyond and independent of the conclusions drawn from individual experimental manipulations. In summary, using a multimodal approach, we aimed to delineate and characterise the brain networks that are functionally coupled with two core regions for skilled object and pattern recognition: bilateral pMTG and CoS.

2. Methods

2.1. Definition of the seed regions

The regions of interest ("seeds") for the present investigation were derived from three previous fMRI studies contrasting chess experts and novices while performing typical task requiring chess-specific object (identification task) and pattern (visual search tasks) recognition (Bilalić, Kiesel, et al., 2011; Bilalić et al., 2010, 2012). Specifically, Bilalić et al. (2011) identified the right pMTG as specifically associated with skilled object recognition by contrasting brain activity in experts versus novices during the identification of chess pieces and their functions (identity and check tasks) with that during the identification of neutral (non-chess) stimuli such as geometrical shapes. In contrast, the left pMTG was involved in object-related processing in experts and novices alike. Further, Bilalić et al. (2010; 2012) identified the bilateral CoS as specifically associated with skilled pattern recognition by contrasting brain activity in experts versus novices during a search for specific pieces in regular chess positions with that during a search for the same kind of chess pieces in random (scattered and meaningless) positions. All four seed clusters are depicted in Fig. 1.

2.2. Resting-state functional connectivity analysis

Each of our four seeds was included in a whole-brain RSFC analysis to examine their specific and common FC patterns across the entire brain.

2.2.1. Sample

The analysis included resting-state fMRI data from 132 adults ranging from 18 to 85 (*M* = 42.3) years of age. All participants (41% female) were without any record of neurological or psychiatric disorders and gave their written informed consent to the study. These data were selected from the datasets included in Biswal et al. (2010) as part of the Nathan S. Kline Institute/Rockland (Orangeburg, NY, USA) data sharing initiative made publicly available via the 1000 Functional Connectomes Project (http://fcon_1000.projects.nitrc.org). The analysis of the data for the current study purposes was approved by the local ethics committee of the Heinrich Heine University Düsseldorf.

2.2.2. Data acquisition and preprocessing

Gradient-echo echo-planar imaging at 3 T (Siemens Trio) was used to record blood oxygen level–dependent (BOLD) activity in 38 transversal slices covering the entire cerebrum. The dataset comprised 260 volumes acquired using the following measurement parameters: repetition time = 2.5 s, echo time = 30 ms, flip angle = 80°, resolution = 3.0 × 3.0 × 3.0 mm^3 voxel size; interleaved slice acquisition order (0.33 mm gap between slices). Participants lay supine in the scanner and were instructed to keep their eyes open and let their mind wander.

All data were preprocessed and analysed using SPM8 (www.fil.ion.ucl.ac.uk/spm). Four dummy scans, which preceded image acquisition to allow for magnetic field saturation, were discarded prior to further analysis. Images were first corrected for head movement by affine

registration using a two-pass procedure by which images were initially realigned to the first image and subsequently to the mean of the realigned images. Each participant's mean image was then spatially normalized to the Montreal Neurological Institute (MNI) single-subject template brain using the "unified segmentation" approach (Ashburner & Friston, 2005), and the ensuing deformation was applied to the individual volumes. Hereby, volumes were resampled at 1.5 × 1.5 × 1.5 × mm^3 voxel size. Images were then smoothed by a 5-mm full-width at half-maximum Gaussian kernel to meet the requirements of the general linear model and compensate for residual anatomical variation.

2.2.3. Data analysis

RSFC measures can be influenced by several confounds such as head movements and physiological processes (e.g., fluctuations due to cardiac and respiratory cycles; cf. Fox et al., 2009; Weissenbacher et al., 2009). In order to reduce spurious correlations, variance explained by the following nuisance variables was removed from each voxel's BOLD signal time series (Langner et al., 2014; Satterthwaite et al., 2013): (i) the six motion parameters derived from the image realignment; (ii) the first derivatives of the six motion parameters, (iii) mean gray-matter, white-matter, and cerebrospinal-fluid signal intensity per time point as obtained by averaging across voxels attributed to the respective tissue class in the SPM8 segmentation. All nuisance variables entered the regression model as first- and second-order terms, resulting in a total of 30 nuisance regressors. After confound removal, data were band-pass filtered preserving frequencies between 0.01 and 0.08 Hz, as meaningful resting-state correlations will predominantly be found in these frequencies given that the BOLD response acts as a low-pass filter (Biswal, Yetkin, Haughton, & Hyde, 1995).

The time course of each seed region's BOLD signal was then extracted for each participant as the first eigenvariate of activity in all gray-matter voxels located within the respective cluster (cf.

Jakobs et al., 2012; Langner et al., 2015). For each participant, the time-series data of each seed region were correlated with the time-series data of each gray-matter voxel in the brain. The resulting voxel-wise Pearson correlation coefficients were transformed into Fisher's *Z* scores. These scores were fed into second-level repeated-measurement analyses of variance. For testing group-level differences in positive RSFC, difference contrasts were inclusively masked with the positive main effect of the respective minuend via conjunction analysis using the strict minimum *t*-statistic (Nichols, Brett, Andersson, Wager, & Poline, 2005). Commonalities among the seeds were examined via minimum-statistics conjunction analyses across the positive or negative group-level main effects for the given seeds. Results were regarded significant if they passed a cluster-level threshold of $p < .05$ [family-wise error (FWE)–corrected for multiple comparisons across the brain; voxel-level height threshold: $p < .001$).

2.3. Meta-analytic connectivity modelling (MACM)

MACM offers an alternative approach to investigating whole-brain FC of a given seed region by way of meta-analytically delineating the co-activation pattern of the seed across published functional imaging results (Eickhoff et al., 2011; Fox et al., 2014). The rationale of this approach is based on the notion that FC is reflected in the correlation of activity in spatially distinct brain regions. That is, regions that are functionally connected should co-activate above chance in functional neuroimaging studies. In contrast to RSFC, which reflects within-subject associations between task-unconstrained activity time courses of distinct brain regions, MACM provides a complementary measure of FC reflecting the across-study likelihood of co-activations with the seed during the performance of structured tasks (albeit without regard to the particular nature of the tasks).

2.3.1. Sample

All MACM analyses were performed using the BrainMap database (www.brainmap.org; Laird et al., 2009). From that database, we included only those experiments that reported coordinates in standard stereotaxic space from normal functional mapping studies (i.e., no interventions such as pharmacological challenges or practice, and no interindividual-differences analyses) in healthy participants using either fMRI or positron emission tomography. Apart from these criteria, we refrained from any pre-selection based on descriptive BrainMap meta-data (i.e., taxonomic categories). In total, this yielded 7572 eligible experiments at the time of analysis.

Filtering the BrainMap database for experiments that reported at least one focus of activation in the given seed regions, we found: (1) 66 experiments reporting activation in the left CoS cluster (in total: 1111 foci, 914 participants); (2) 56 experiments reporting activation in the right CoS cluster (732 foci, 748 participants); (3) 105 experiments reporting activation in the left pMTG cluster (2028 foci, 1443 participants); and (4) 101 experiments reporting activation in the right pMTG cluster (2597 foci, 1304 participants).

2.3.2. MACM algorithm

Task-based FC (i.e., co-activation) patterns for each of the four seed regions were computed following established procedures (Bzdok et al., 2013; Genon et al., 2017): For each seed region, a separate quantitative meta-analysis across all foci reported in the experiments retrieved for the given seed (cf. above) was performed to assess how likely any other voxel throughout the brain co-activated with the given seed region. As all experiments entering this analysis were selected based on their reporting activation in the given seed, highest convergence will naturally be observed in the seed region. Significant convergence of other activation foci, however, would indicate consistent across-study co-activation (i.e. task-based FC) with the seed. Meta-analysis was performed using

the revised version of the activation likelihood estimation (ALE) approach (Eickhoff, Bzdok, Laird, Kurth, & Fox, 2012; Turkeltaub et al., 2012). This algorithm treats activation foci reported from a given experiment as centers of 3-D Gaussian probability distributions that reflect the spatial uncertainty associated with neuroimaging results. The probability distributions of all reported foci were combined into a modeled activation map for each experiment. The voxel-wise union of these modeled activation maps across all experiments associated with a given seed then yielded an ALE score for each voxel of the brain describing the co-activation probability of that particular location with the seed.

Significance of these co-activation probabilities is then computed by comparison with an analytical null-distribution as described in Eickhoff et al. (2012). In short, this null-distribution reflects the distribution of ALE scores under the null-hypothesis of a random spatial association across experiments. The *p*-value of a "true" ALE score was then given by the proportion of equal or higher values under the null distribution. ALE maps were thresholded at cluster-level $p < .05$ (FWE-corrected; voxel-level height threshold: $p < .001$).

Difference maps comparing task-based FC of two given seeds were obtained by first calculating voxel-wise *z*-score differences between two individual MACM maps. The experiments contributing to either MACM analysis were then pooled and randomly divided into two groups of the same size as the sets of contrasted experiments (Eickhoff et al., 2011). Voxel-wise ALE scores for these two randomly assembled groups were subtracted from each other and recorded. Repeating this process 10,000 times yielded an empirical null-distribution of ALE score differences between the two conditions. Based on this permutation procedure, the map of true differences was then thresholded at a posterior probability of $P > 0.95$ for a true difference between the two samples. The resulting maps were then masked with the respective main effect of the minuend connectivity map to avoid obtaining significant FC differences in voxels that do not show significant co-activation in

the underlying connectivity map. Commonalities among the seeds regarding task-based FC were examined via minimum-statistics conjunction analyses across the MACM maps of individual seeds. In practice, regions significantly connected with two (or more) seeds were delineated by computing the intersection of the (cluster-level FWE-corrected) connectivity maps obtained from the individual MACM analyses of the seeds involved. Furthermore, for both MACM difference and conjunction maps, only clusters with at least 20 contiguous voxels were considered relevant.

2.4. Commonalities across RSFC and MACM analyses

For delineating areas that showed consistent task-independent and task-constrained FC with a given seed, we performed minimum-statistics conjunction analyses across corresponding RSFC and MACM analyses. That is, for each seed region, we identified those voxels that showed significant positive FC with a given seed in the task-independent state (RSFC) as well as in the task-constrained state (MACM). This way, we sought to elucidate the state-independent FC core network of each seed. Such across-state consistency in FC patterns was delineated by computing the intersection of the (cluster-level FWE-corrected) FC maps obtained from the two analyses involved, respectively. In the resulting "consensus maps," only clusters consisting of at least 10 contiguous voxels were considered relevant. These consensus maps were computed for all main effects, differences, and conjunctions; they constitute the main focus of this study.

2.5. Quantitative functional profiling

In order to quantitatively assess the functional significance of our four seed regions, we analysed their correspondence with descriptors for cognitive processes as provided by the BrainMap database (www.brainmap.org; Laird et al., 2009). This database contains meta-data that describe the behavioural domain and paradigm class of each experimental contrast included according to a pre-specified taxonomy {Fox, 2005 #1063; see www.brainmap.org/scribe). By filtering this database

for experiments featuring activation within a given region of interest and performing statistical analysis on the descriptors of the selected experiments, functional roles of individual regions may then be characterized in an objective manner.

We analysed the functional descriptors of BrainMap experiments associated with assessed network nodes by way of forward inference {Bzdok, 2013 #997}(Eickhoff et al., 2011). To this end, we used binomial tests to identify behavioural domains and paradigm classes, respectively, for which the probability of activation in the given seed region was significantly above chance. That is, we tested whether the probability of finding activation in voxels of interest given a particular behavioural domain or paradigm class [P(Activation | Descriptor)] was higher than the baseline probability of finding activation in those voxels across the entire database [P(Activation)]. Results were considered significant at $p < .05$, corrected for multiple comparisons by thresholding the false-discovery rate (FDR). However, given the rather low baseline probabilities for finding activations in our relatively small seeds (cf. section 2.3.1), this test is conservative. To reduce the risk of false negative results due to over-conservativeness, we also report significant results (at $p < .05$) before FDR correction.

To examine the specificity of the functional profiles of the four seed regions, we performed contrast analyses, which were restricted to those experiments in BrainMap that activated either set of seeds. Thus, these difference analyses inherently are somewhat less conservative than the tests for main effects against the entire database, as described above. For differential forward inference, we compared the activation probabilities between two seeds given a particular behavioural domain or paradigm class, respectively (Bzdok et al., 2013; Eickhoff et al., 2011). The results of these quantitative comparisons were thresholded at $p < .05$ (FDR-corrected for multiple comparisons).

3. Results

The following sections present the results of our FC and functional profiling analyses for each of the four seed regions (see Fig. 1). FC results will generally be restricted to common findings across both measurement modalities (i.e., RSFC and MACM; cf. section 2.4). First, we report main effects for all four seed regions individually, followed by *inter*hemispheric conjunction and difference analyses of homotopic seeds (i.e., left/right pMTG as well as left/right CoS) and, subsequently, analogous *intra*hemispheric analyses of the two seed regions in each hemisphere (i.e., left pMTG/CoS as well as right pMTG/CoS).

For each seed, RSFC analyses revealed more extended networks of functionally connected regions than did MACM. Thus, all consensus maps were constrained by the more circumscribed results of the latter, thereby essentially mirroring the MACM-only findings. We, therefore, also present the RSFC-only results for two particularly relevant analyses: the contrast between left and right pMTG and the conjunction across all four seeds. The former analysis was motivated by our specific expectation of interhemispheric differences in pMTG RSFC based on differential expertise effects on regional left or right pMTG activity in line with the "double-take" hypothesis of expertise (cf. Bilalić et al., 2010; 2011). The latter analysis, in turn, was done to reduce the risk of false negatives due to the strictness of the conjunction across four consensus maps (i.e., across eight individually significant FC maps).

3.1. Main effects for individual seed regions

3.1.1. pMTG

The connectivity pattern for our left pMTG seed region, as revealed across both RSFC and MACM analyses, comprised six clusters (Fig. 2): (i) left and (ii) right pMTG extending medially into fusiform gyrus (FusG) and laterally into area V5 and posterior inferior temporal gyrus (pITG);

(iii) left posterior inferior frontal gyrus (IFG; dorsal area 44) extending to left ventral premotor cortex; (iv) left intraparietal sulcus extending into superior parietal lobule; (v) left anterior insula; and (vi) left mid-dorsal IFG [ventral Brodmann area (BA) 46].

For the right pMTG seed, we observed significant FC with a similar, but mainly oppositely lateralized and more extended set of nine clusters (Fig. 2): (i) right pMTG, extending medially into FusG and laterally into area V5, pITG, as well as posterior superior temporal gyrus (pSTG); (ii) left pMTG extending medially into FusG and laterally into area V5 and pITG; (iii) right posterior IFG (dorsal area 44) extending to right ventral premotor cortex; (iv) right and (v) left supramarginal gyrus (SMG); (vi) right and (vii) left intraparietal sulcus and adjacent superior parietal lobule; (viii) right inferior frontal sulcus extending into the middle frontal gyrus (ventral BA 46); and (ix) right anterior insula.

3.1.2. CoS

The FC pattern for our left CoS seed region, again as revealed across both RSFC and MACM analyses, comprised four clusters (Fig. 3): (i) left and (ii) right CoS, each extending to ipsilateral FusG and hippocampus; (iii) left and (iv) right ventral posterior cingulate cortex (sometimes labeled as retrosplenial cortex; cf., e.g., Epstein, 2008), each extending posteriorly across the parieto-occipital sulcus into ipsilateral cuneus.

The FC pattern for the right CoS seed comprised five clusters (Fig. 3). The first four clusters largely overlapped with those observed for the left CoS (cf. above), though the cluster centering on the right CoS extended substantially more anteriorly into the hippocampus as well as postero-laterally into area V5/pITG. The only additional cluster was located in left middle occipital gyrus.

3.2. Interhemispheric comparisons of homotopic seed regions

3.2.1. pMTG

The above connectivity analyses revealed strongly lateralized clusters for either pMTG seed. This impression was corroborated by a conjunction analysis, which revealed only limited overlap between both connectivity patterns: across left and right pMTG, both RSFC and MACM analyses indicated common FC with three clusters: (i) left and (ii) right pMTG extending into pITG, and (iii) a small cluster in left intraparietal sulcus and adjacent superior parietal lobule (Fig. 2).

Expectedly, contrasting left and right pMTG seeds across both FC measurement modalities yielded selectively increased FC for left pMTG with adjacent cortex extending to pITG, left FusG, left posterior IFG (dorsal area 44) extending to ventral premotor cortex, and the most posterior aspects of right ITG/MTG (covering parts of right area V5). The opposite contrast yielded selectively increased FC for right pMTG with adjacent cortex extending to pSTG, ventral premotor cortex, and posterior IFG (dorsal area 44).

When considering RSFC analyses only, the contrast between left and right pMTG revealed selectively increased connectivity for the left pMTG seed with an extensive bilateral (though left-dominant) network (Fig. S1). Bilaterally, this network comprised superior parietal cortex, intraparietal sulcus and dorsal precuneus; primary and secondary somatosensory cortex; inferior, middle and superior occipital gyrus; lateral occipital cortex extending into inferior temporal gyrus; central insula; mid-cingulate cortex; ventral and dorsal premotor cortex; anterior IFG and middle frontal gyrus; as well as anterior and posterior ventral cerebellum (lobule VII and VIII). Unilaterally, selectively increased FC in the left hemisphere was found with anterior insula, posterior IFG (area 44), posterior cingulate cortex, as well as FusG; and in the right hemisphere with the dorso-posterior cerebellum (lobule VI). The opposite contrast yielded selectively increased RSFC for the right pMTG seed with a less extensive, mainly right-lateralized network (Fig. S1). In

the right hemisphere, this network consisted of four clusters: pMTG extending into inferior parietal cortex and anteriorly almost along the entire MTG and adjacent superior temporal sulcus up to the temporal pole; anterior ITG; precuneus; and a large frontal cluster extending from dorsal to ventral premotor cortex and posterior IFG into frontal operculum and posterior orbitofrontal cortex. In the right hemisphere, we found selectively increased RSFC with the right pMTG seed in pMTG and pSTG as well as posterior cerebellum (lobule VII).

3.2.2. CoS

The FC analyses for each individual CoS seed revealed highly similar clusters. This impression was corroborated by a conjunction analysis: across left and right CoS, both RSFC and MACM analyses jointly indicated common connectivity with four clusters (Fig. 3): (i) left and (ii) right CoS extending to FusG and hippocampus; (iii) left and (iv) right ventral posterior cingulate cortex extending to anterior cuneus.

Contrasting left versus right CoS across both FC modalities yielded selectively increased FC for left CoS with adjacent FusG and hippocampus. The opposite contrast analogously yielded selectively increased FC for right CoS with adjacent FusG and hippocampus, but this cluster extended more anteriorly than the corresponding one for left CoS.

3.3. Intrahemispheric analyses: Commonalities and differences between pMTG and CoS

3.3.1. Left hemisphere

A conjunction analysis across the connectivity patterns of left-hemispheric pMTG and CoS seeds, as observed in both RSFC and MACM analyses, did not reveal any significant overlap. Contrasting left pMTG with left CoS across both FC modalities yielded selectively increased FC for pMTG with adjacent cortex extending to pITG as well as with homotopic right pMTG/pITG, left

FusG, left posterior IFG (dorsal area 44) extending to ventral premotor cortex, left intraparietal sulcus, and left anterior insula (Fig. 4A). This pattern thus corresponded largely with the main effect of left pMTG whole-brain FC. A similar correspondence was observed for left CoS: in comparison with left pMTG, connectivity of CoS was selectively increased with adjacent and homotopic parts of CoS extending to FusG and hippocampus (more extensively in the left hemisphere), as well as bilateral ventral posterior cingulate cortex extending into cuneus (Fig. 4A).

3.3.2. Right hemisphere

A conjunction analysis across the connectivity patterns of right-hemispheric pMTG and CoS, as observed in both RSFC and MACM analyses, revealed a single cluster of overlap in right area V5/pITG (Fig. 5). Contrasting right pMTG versus CoS across both FC modalities yielded selectively increased FC for right pMTG with adjacent pMTG, pITG, and pSTG as well as left pMTG/pITG, right posterior IFG (dorsal area 44) extending to ventral premotor cortex, bilateral supramarginal gyrus, right intraparietal sulcus, and right anterior insula (Fig. 4B). This pattern again corresponded largely with the main effect of right pMTG FC. A similar correspondence was also found for right CoS again: the opposite contrast yielded selectively increased FC for right CoS with bilateral CoS extending to FusG and hippocampus (substantially more extensively in the right hemisphere), bilateral ventral posterior cingulate cortex extending into cuneus, and left middle occipital gyrus (Fig. 4B).

3.4. Conjunction analysis across all four seed regions

There was no brain region that showed significant FC with all four seed regions across both RSFC and MACM analyses. When considering RSFC only, all four seeds showed significant positive FC with an extensive bilateral temporo-parieto-occipital network (Fig. 6). This network included

pMTG, FusG (extending in the right hemisphere into posterior and middle ITG), precuneus, and medial superior parietal cortex as well as inferior, middle and superior occipital gyrus. A further cluster was observed in left medial cerebellum (lobules VII and VIII).

3.5. Meta-analytic functional profiling

3.5.1. Main effects for individual seed regions

Left pMTG activity was most strongly associated with semantic aspects in language processing as well as paradigms requiring tone or face monitoring/discrimination (see Table 1 for further, less strong functional associations that did not survive correction for multiple comparisons). For right pMTG activity, an association with the "go/no-go" paradigm, which taxes inhibitory cognitive control, was the only one to survive multiple-comparison correction, but there were several uncorrected significant associations with tasks involving visual attention, cued explicit recognition, face discrimination, or film viewing (see Table 1 for a full list of functional associations). Activity in our left CoS seed was most strongly associated with "passive viewing" paradigms (see Table 1 for further functional associations), while activity in right CoS was most strongly associated with the "visual shape perception" domain as well as "passive viewing" and "overt naming" paradigms (see also Table 1).

3.5.2. Functional differences between seed regions

Contrasting functional associations with left and right pMTG yielded stronger associations of left pMTG activity with semantic language processing and affective processing as well as paradigms involving semantic monitoring/discrimination (see Fig. S2). Conversely, right (vs. left) pMTG activity was more strongly linked to action inhibition and to paradigms taxing visuospatial attention, visual distractor processing, or response inhibition ("go/no-go tasks"). The analogous

comparison between left and right CoS revealed no significantly stronger associations for left (vs. right) CoS, but activation in right (vs. left) CoS was more strongly linked to visual shape perception as well as paradigms involving face perception (Fig. S2).

Contrasting functional associations with left pMTG and left CoS revealed a stronger association of left pMTG activity with paradigms involving tone or face monitoring/discrimination or film viewing, while activity in left CoS was more strongly linked to social cognition and "passive viewing" paradigms (see Fig. S3). The analogous comparison between right pMTG and right CoS yielded stronger associations of right pMTG activity with action execution as well as paradigms involving "film viewing." Conversely, right CoS (vs. pMTG) activity was more strongly linked to visual (shape) perception, processing semantic aspects in language, and emotion as well as "passive viewing," "overt naming," and "reward" paradigms (Fig. S3).

4. Discussion

We investigated the functional networks in which two core regions for skilled object and pattern recognition, bilateral pMTG and CoS, are embedded. The pMTG was found to be part of an extensive network, linking the ventral visual stream (including region V5 involved in motion perception) with parietal and prefrontal regions for action planning and action preparation. The functional connections of pMTG showed strong lateralization effects, which were most strongly pronounced in the less conservative RSFC-only analysis: Left pMTG was preferentially connected to an extensive and rather symmetrical network associated with planning and preparing visually guided actions, while right pMTG was preferentially connected with the entire right MTG up to its anterior pole, presumably involved in semantic processing using conceptual knowledge (Clos et al., 2014; Rice, Lambon Ralph, & Hoffman, 2015; Wright, Stamatakis, & Tyler, 2012; Xu et al., 2015). The CoS seeds were predominantly connected with their contralateral homotopic counterparts as

well as hippocampus and RSC/posterior cingulum, showing hardly any lateralization effects. Thus, relative to pMTG, left and right CoS appear to be embedded in less extensive, largely overlapping bilateral functional networks.

The conservative conjunction analysis across the connectivity patterns of all 4 seed regions did not yield any significant overlap, but when the analysis was based on RSFC only, we found a substantial amount of network overlap forming a bilateral symmetrical 'triangle' connecting ventral and dorsal visual streams. That is, at least in the task-unconstrained state, all 4 regions were strongly coupled with each other as well as with regions associated with processing both "what" and "where" aspects of visual input. Finally, meta-analytic functional profiling revealed a specific association with semantic and affective processing for left pMTG, and with action inhibition and attention for right pMTG. Right CoS, in turn, was specifically associated with shape and face perception, whereas left CoS, while being linked to passive viewing in general, showed no stronger association with any functional descriptor than did its right-hemisphere counterpart.

4.1. Skilled object recognition

Skilled object recognition refers to the superior identification of objects in a particular domain of expertise, which typically goes along with recognizing the object's function and associated object-specific actions as well as perceiving the object in relation to other domain-specific objects (in our case, pieces on the chessboard). The FC patterns of right and left pMTG shed some light on the specific role of this brain region in mediating these processes, and they also provide insight into the neural implementation of expertise in general. Experts regularly engage brain areas in both hemispheres in tasks that are typically linked with lateralized brain activity in novices, such as performing mental calculations (Pesenti et al., 2001) or calculations with an external device like an abacus (Hanakawa, Honda, Okada, Fukuyama, & Shibasaki, 2003), or looking for abnormalities in

radiological images (Bilalić, Grottenthaler, Nägele, & Lindig, 2016; Haller & Radue, 2005). The same phenomenon, that is, a smaller hemispheric asymmetry of task-related brain activity, has been uncovered in our previous studies with chess experts (Bilalić et al., 2010, 2012), and in particular related to skilled object perception (Bilalić, Kiesel, et al., 2011). While both experts and novices recruited the left pMTG during object recognition, experts additionally activated the right pMTG. This is referred to as the "double take of expertise" (Bilalić, 2017) because of the territorial properties of the phenomenon in the brain. Current theories (Bilalić, 2017) assume that the skill-related retrieval of domain-specific knowledge during seemingly effortless perception recruits additional neural resources in experts. The activation of analogous (homotopic) areas in the other hemisphere appears to be the brain's typical way of dealing with demanding tasks (Weissman & Banich, 2000). More specifically, the double take of expertise may reflect independent parallel processing of task subcomponents, or their highly dependent processing through inter-hemispheric interaction, or a mixture of both mechanisms. In case of the pMTG, the additional right-lateralized recruitment in experts might be facilitated by the generally strong interhemispheric FC observed between left and right pMTG (see Fig. 2). It remains to be tested, though, whether this functional coupling is further enhanced in experts.

The strong interhemispheric coupling between bilateral pMTG may form one basis of skilled object perception – another may be the right pMTG's connectivity with other brain areas. Both left and right pMTG seeds were found to be significantly connected with ipsilateral fronto-parietal areas (see Fig. 2), which may mediate stable object "affordances" (i.e., action representations closely associated with a given object) as part of skilled object perception (Binkofski & Buccino, 2006; Binkofski, Buccino, Zilles, & Fink, 2004; Sakreida et al., 2016). In fact, the observed connectivity pattern represents major parts of the so-called "tool network" (Lewis, 2006; Valyear, Fitzpatrick, & McManus, 2017). This network is recruited during the

perception of tools and the execution of tool-related actions. Along the same lines, studies on pMTG functional connectivity (Bracci, Cavina-Pratesi, Ietswaart, Caramazza, & Peelen, 2012; Hutchison, Culham, Everling, Flanagan, & Gallivan, 2014) revealed connectivity profiles similar to the one observed here and support the idea that our seed region constitutes the tool-selective part of pMTG, where tools (i.e., graspable objects with well-defined functions) are preferentially represented. The tool network incorporates semantic knowledge about tool functions and tool–action associations through extensive experience with tools. It is very likely that for chess experts, chess pieces become "tools," as with experience these objects become strongly associated with specific functional actions, such that in the minds of chess experts there is no way a given piece could have any other way of moving than it normally does. Collectively, this suggests that skilled object perception in chess consists in part of processing chess pieces like "tools" for achieving particular goals by executing highly overlearned object-specific movements. Hence, automatically construing a given chess scenario in terms of actions afforded by its constituent pieces might strongly contribute to the capability of chess masters to grasp the gist of a complex multi-object game situation and find a good next move within a few seconds.

While the connections of left pMTG were confined to its own hemisphere (apart from the aforementioned connection to the homotopic right pMTG), the right pMTG showed additional interhemispheric connections with left intraparietal sulcus and left SMG. The bilateral intraparietal sulcus is linked to the goal-oriented control of spatial attention (Corbetta, Patel, & Shulman, 2008). Its strong coupling with right pMTG may subserve the rule-based guidance of visual attention according to the identity of the given object and its potential move trajectories. We conjecture that this interregional connectivity may facilitate move planning in chess experts by way of relaying object-specific semantic information (e.g. object trajectories) stored in temporal cortex via SMG to the dorsal attention system in order to help it direct attention to inconspicuous but informative

locations in the scene, such as crossings between imaginary object paths from which several objects could be controlled (Bilalić et al., 2010). The bilateral SMG is particularly important in the context of skilled object recognition because experts, but not novices, engage these areas when they need to explicitly relate objects to each other based on the actions (i.e., moves) that can be performed with the objects (e.g., to detect if a chess piece is threatened by another). The SMG is associated, among other things, with the explicit retrieval of the function of tools (Johnson-Frey, 2004), and is considered to be a major node in the ventral branch of the dorsal visual stream, subserving knowledge-based aspects of action representation (Binkofski & Buxbaum, 2013). In this framework, the ventral branch (connecting SMG with ventral premotor cortex) has been proposed to represent a "use" pathway for tools, subserving the long-term storage of particular skilled actions associated with familiar objects. Information to this pathway can be provided by the pMTG.

As only the right pMTG was found to be connected to both left and right SMG, its additional recruitment in experts may be crucial for mediating the efficient interplay between pMTG and bilateral SMG during expertise-related tasks. This in turn might enable the superior perception of domain-specific objects and their functions, particularly in complex situations like move choice in chess as both right and left SMG appear to be necessary for performing naturalistic multi-step tasks involving several objects (Hartmann, Goldenberg, Daumuller, & Hermsdorfer, 2005). Furthermore, in line with these implications, it has been shown that the right (vs. left) ventral premotor cortex, which we found to be selectively connected with right pMTG (see Figures 2 and S1), is predominantly recruited for the imagery of movement characteristics in space, as compared with the imagery of egocentric movements (Binkofski et al., 2000). This reasoning about a specific role of right (vs. left) pMTG in guiding attention and action-related cognition for better object perception is corroborated by our meta-analytic functional characterization, which showed that right

(vs. left) pMTG activity was more strongly associated with demands on visuospatial attention, visual distractor processing, and response inhibition.

Taken together, our findings agree with the above-mentioned "double take" account of expertise, which posits that experts capitalize on a complementary usage of the division of labor between the hemispheres. Our data indicate that experts, additionally recruiting the right-hemisphere pMTG for object identification, employ a region that is more widely and more bilaterally connected than its left-sided counterpart. We hypothesize that this connectivity pattern, in turn, enables experts to quickly connect object identification with potential object actions in space (i.e., tool use), ultimately leading them to "see" good moves immediately without substantial delays arising from serial processing as performed by novices. As chess objects are in many ways similar to other man-made objects such as tools (Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995), being visually distinctive and having specific functions rooted in movement, we would argue that our findings provide insights into the neural mechanisms behind perceiving familiar objects in general: They suggest that the bilateral pMTG, demonstrating substantial connectivity with both upstream areas of the (ventro-)dorsal visual stream (e.g., SMG) and action-related areas (e.g., premotor cortex), constitutes a crucial gateway for efficiently linking the identity of objects with their functions and thereby implicated actions.

4.2. Skilled pattern recognition

The bilateral CoS is involved in skilled pattern recognition, that is, perceiving numerous objects and their spatial relations. Left and right CoS are heavily interconnected with each other (Fig. 3) but also with the neighboring areas (hippocampus, FusG), and posterior cingulate/cuneus. All these areas are related to memory processes and have been implied in the research on skilled pattern perception (Bilalić et al., 2010, 2012; Campitelli, Gobet, Head, Buckley, & Parker, 2007; Wan et

al., 2011). This might not come as a surprise because the CoS is a part of the parahippocampal place area (PPA; Epstein & Kanwisher, 1998), an area that is believed to be involved in scene perception (Epstein, 2008). The FusG, and particularly the fusiform face area, have also been found to be involved in skilled pattern perception (Bartlett, Boggan, & Krawczyk, 2013; Bilalić, Langner, et al., 2011; Krawczyk, Boggan, McClelland, & Bartlett, 2011) but not necessarily object perception (Bilalić, 2016).

Beside the interconnection between the bilateral CoS and adjacent areas, both left and right CoS were also connected to left and right posterior cingulate cortex, sometimes also called retrosplenial cortex (RSC; Epstein, 2008). The RSC is believed to support spatial orientation in the environment (Epstein, 2008) and, just like the parahippocampal place area, is also involved in scene perception (Epstein, 2008). Similarly, our studies (Bilalić et al., 2012) and those of others (Bartlett et al., 2013; Wan et al., 2011), demonstrated the involvement of the RSC is skilled pattern perception. Again, the bilateral interconnections between CoS and RSC confirm the engagement of bilateral brain areas in expertise.

Intriguingly, the posterior cingulum/"RSC" is a node of the brain network involved in theory-of-mind (ToM) cognition, which refers to understanding the intentions of others (cf. Bzdok et al., 2012). Indeed, taking into account the opponent's plans is an essential part of playing chess. The robust FC of bilateral CoS with this posterior medial brain region may, therefore, reflect the social component of chess and not purely spatial, pattern-related processing. By putting themselves in the adversary's position, chess experts may more efficiently detect threats and understand the functional nature of the relations between individual chess objects. Furthermore, the ventral posterior cingulum of monkeys has been found to code subjective target utility (McCoy & Platt, 2005) and integrate individual outcomes across decision making for strategy modification in changing environments (Pearson, Hayden, Raghavachari, & Platt, 2009). In humans it was shown to

be connected to the laterobasal amygdala, likely involved in scanning perceptual input for biological significance (Bzdok et al., 2015). This and other evidence led to the proposal that this posteromedial brain region subserves an evaluative function with respect to features of perceived or imagined stimuli (cf. Bzdok et al., 2015). Our data, in turn, lead us to speculate that pattern recognition processes in the CoS might be importantly informed by evaluative signals from ventral posterior cingulum/RSC, partly derived from taking the adversary's perspective.

Unlike pMTG, where novices engaged the left part to an extent comparable with experts, activity in both left and right CoS and RSC was previously found to be clearly modulated by expertise (Bilalić et al., 2012; Wan et al., 2011). Nevertheless, just like pMTG, right CoS also demonstrated more pronounced FC with other areas than its left counterpart (see Figure 3). Besides neighbouring areas in the same hemisphere (hippocampus and FusG), right CoS was also connected to lateral brain areas in the right (area V5) and left (middle occipital gyrus) hemisphere. The overlap between right CoS and right pMTG in their FC with area V5, a region involved in visual motion perception, may in particular go a long way in explaining the interaction between the object and pattern recognition. This differential functional network architecture of right versus left CoS suggests some functional specificity, beyond the common involvement of bilateral CoS in skilled pattern recognition observed in previous activation studies (Bilalić et al., 2010, 2012; Campitelli et al., 2007). Along the same lines, our meta-analytic functional characterization revealed that right (vs. left) CoS was more consistently linked with visual shape recognition and (skilled) face perception, suggesting a stronger role of right CoS in bringing individual objects and their spatio-functional interrelations together for superior scene perception.

4.3. Connection between skilled object and pattern recognition

Object and pattern recognition are often investigated separately, but it is difficult to imagine that they are independent of each other. The processes involved in object recognition may be the basis for recognizing patterns that the individual objects and the relations between them make. Conversely, the identification of an object may also benefit from recognizing how the object could be affected by another object in the scene (Roberts & Humphreys, 2010). Our results are in line with the notion of object and pattern recognition being strongly interrelated. Indeed, with RSFC we observed a "triangle" of heavily connected brain areas common for both pMTG and CoS seeds, which closely follows dorsal and ventral pathways (see Figure 6).

There are two intriguing implications of possible interactions between the two main pathways. One is the aforementioned connection between the right CoS and the right pMTG (see Figure 3). Unlike the left CoS, the right CoS seems to be significantly aligned with the right pMTG. The other is the only shared cluster between the pMTG and CoS connectivity patterns in the right area V5 (see Figure 5), which is thought to subserve visual motion perception, as alluded to above. The fact that it is an area in near proximity of the pMTG and that it is again right-lateralized point out that this right-hemisphere connectivity may be crucial for explaining the neural implementation of skilled object perception in experts. In particular, the right pMTG may be the information hub for connecting object and pattern processing: On the one hand, it is heavily connected with its left counterpart but also with the SMG bilaterally, areas involved in parsing object-specific move trajectories that define the relations between individual pieces. On the other hand, it is connected to the right CoS, an area crucial for recognizing the (functional) patterns that several objects and their interrelations constitute. Of course, the role of the right pMTG as a hub for the integration of object and pattern recognition processes is hypothetical at this stage. However, the patterns of empirical data fit well with the notion of the right pMTG being of immense importance for experts'

performance in domains where movable objects need to be viewed and identified in a meaningful spatio-functional context to act upon them in an optimal way. Further experiments may directly manipulate specific aspects in object and pattern recognition to pinpoint the unique contribution of the right pMTG in skilled object perception.

4.4. Summary and future perspectives

Our study elucidated the FC patterns of two brain areas, pMTG and CoS, related to skilled object and pattern recognition, respectively. Overall, we found that bilateral pMTG is strongly coupled with regions related to object use and action planning in general, while meta-analytic characterisation indicated an above-chance association of this region with semantic and action-related processing. This supports the notion that skilled visual object recognition is not just about shape identification but should easily include the processing of object functions such as potential object motion trajectories that relate a given object with others. CoS, in turn, was found to be strongly coupled with regions involved in scene perception and perspective taking (ToM cognition), which suggests that skilled pattern recognition in chess may involve social cognition to fully realize and evaluate the patterns of one's own and the adversary's potential object movements and, thus, to detect threats and advantageous move options. Significant associations of CoS with face and shape perception as well as passive viewing, in turn, agree with the assumption that skilled pattern recognition may help object identification in experts.

Previous fMRI studies on expertise frequently revealed "double take" (i.e., bilateral) activation patterns where experts, other than novices, more strongly engaged homotopic regions in the right hemisphere for domain-specific processing. Our study went a step further and demonstrated that the right pMTG may be the information hub that enables the integration of object and pattern recognition processes. In this way our data suggest a model for connecting the areas in the dorsal

visual stream subserving object recognition with the areas in the ventral stream subserving pattern recognition. This calls for further examination in future research. However, beside qualitative differences in network architecture (e.g., additional involvement of contralateral regions), subsequent work should examine whether skilled perception is also rooted in altered coupling strengths between network nodes in task-free and task-driven states. In particular, the question to what degree changes in regional activity and interregional coupling uniquely contribute to performance differences (i.e., mediate different skill levels) constitutes a challenge still to be met. Finally, our study corroborates the usefulness of chess as a model case for neuroscientific research across many functional domains, ranging from perception to action planning and simulation. Due to the presence of an adversary, chess even offers as-yet untapped possibilities as an investigative vehicle for social neuroscience.

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Table

Table 1. Behavioural domains and paradigm classes significantly associated with the seed regions according to forward inference from meta-data of the BrainMap database.

Region	Behavioural Domain	Paradigm Class
Left pMTG	Cognition.Language.Semantics*	Tone Monitor/Discrimination*
	Cognition.Memory.Explicit	Face Monitor/Discrimination*
	Perception.Audition	Cued Explicit Recognition
	Cognition.Language.Speech	Semantic Monitor/Discrimination
	Cognition.Reasoning	Film Viewing
		Encoding
		Reading (Covert)
Right pMTG	Action.Inhibition	Face Monitor/Discrimination
	Cognition.Language.Speech	Go/No-Go
	Perception.Audition	Cued Explicit Recognition
		Film Viewing
		Visual Distractor/Visual Attention
Left CoS	Cognition.Language.Semantics	Passive Viewing*
	Cognition.Social Cognition	Encoding
	Cognition.Memory.Explicit	
Right CoS	Perception.Vision.Shape*	Naming (Overt)*
	Cognition.Memory.Explicit	Passive Viewing*
	Cognition.Language.Semantics	Face Monitor/Discrimination
	Perception.Vision	
	Cognition.Language.Speech	

Note. All associations significant at $p < .05$, uncorrected (* survived FDR-correction for multiple comparisons). pMTG = posterior middle temporal gyrus; CoS = collateral sulcus.

Figure Captions

Fig. 1. Rendering of the four seed regions: bilateral posterior middle temporal gyrus (pMTG) and bilateral collateral sulcus (CoS).

Fig. 2. Significant whole-brain functional connectivity of left (red) and right (blue) posterior middle temporal gyrus (pMTG) across both task-free and task-constrained states.

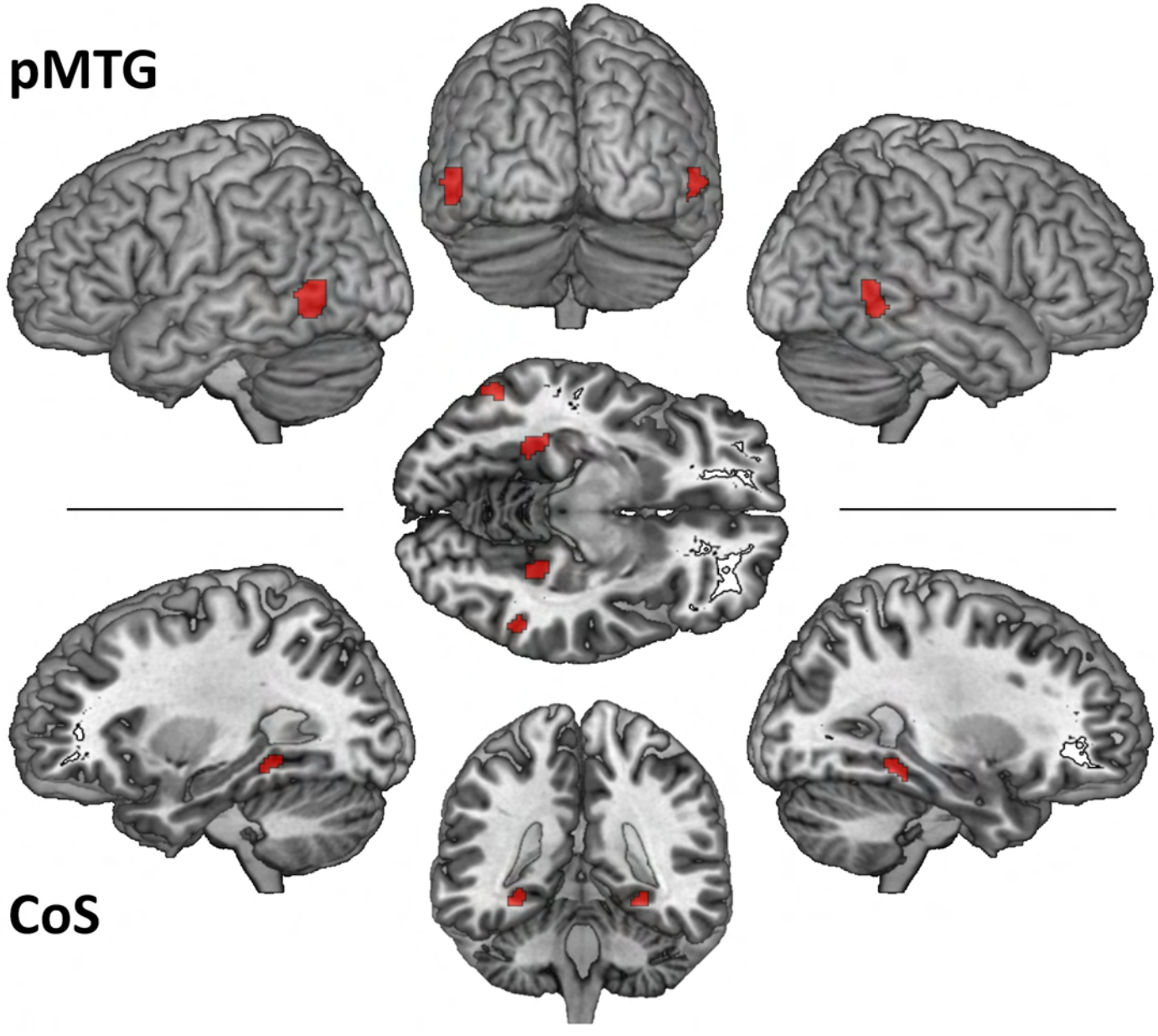
Fig. 3. Significant whole-brain functional connectivity of left (red) and right (blue) collateral sulcus (CoS) across both task-free and task-constrained states.

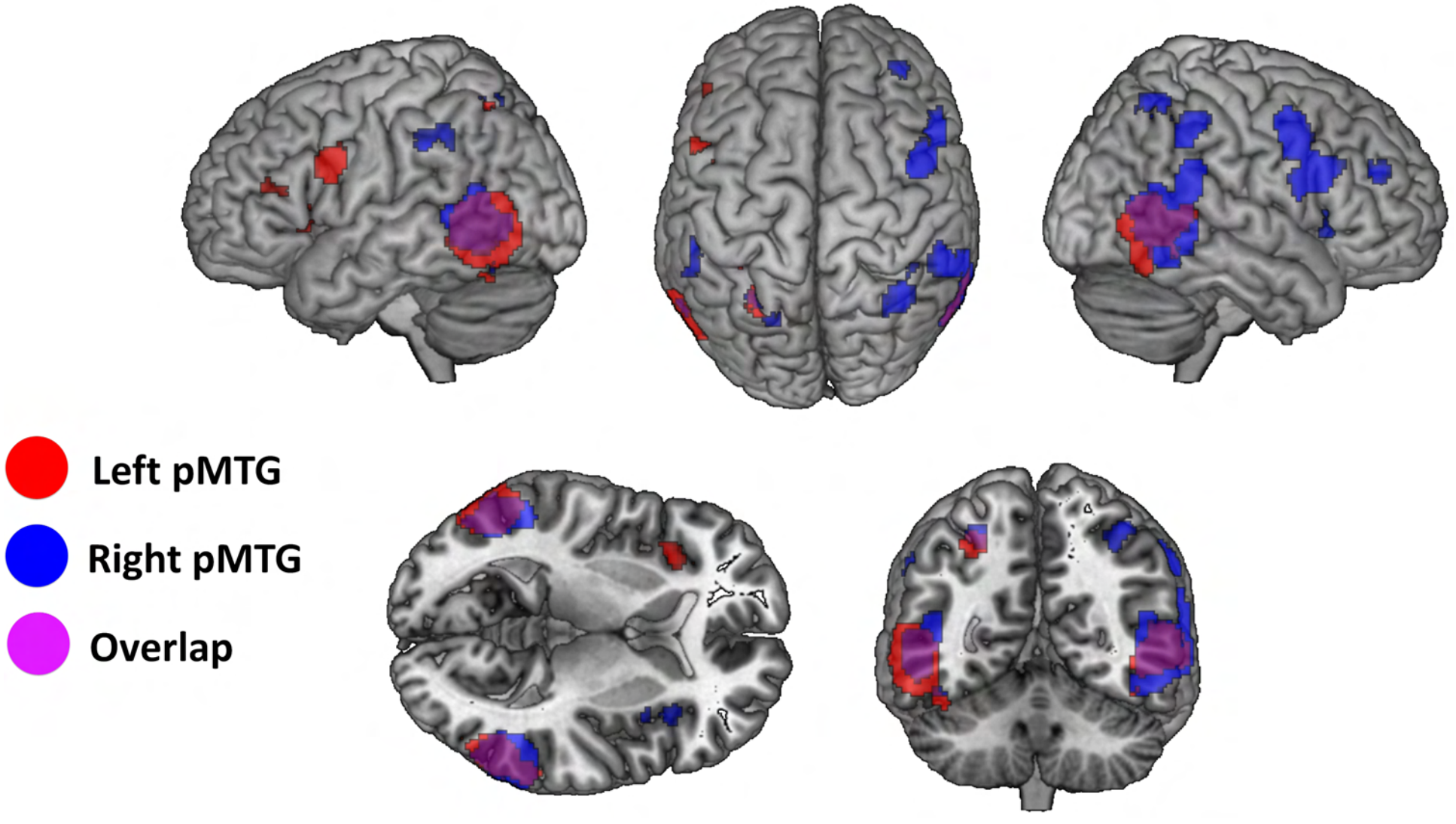
Fig. 4A. Differences in functional connectivity of left posterior middle temporal gyrus (pMTG) and left collateral sulcus (CoS) across both task-free and task-constrained states.

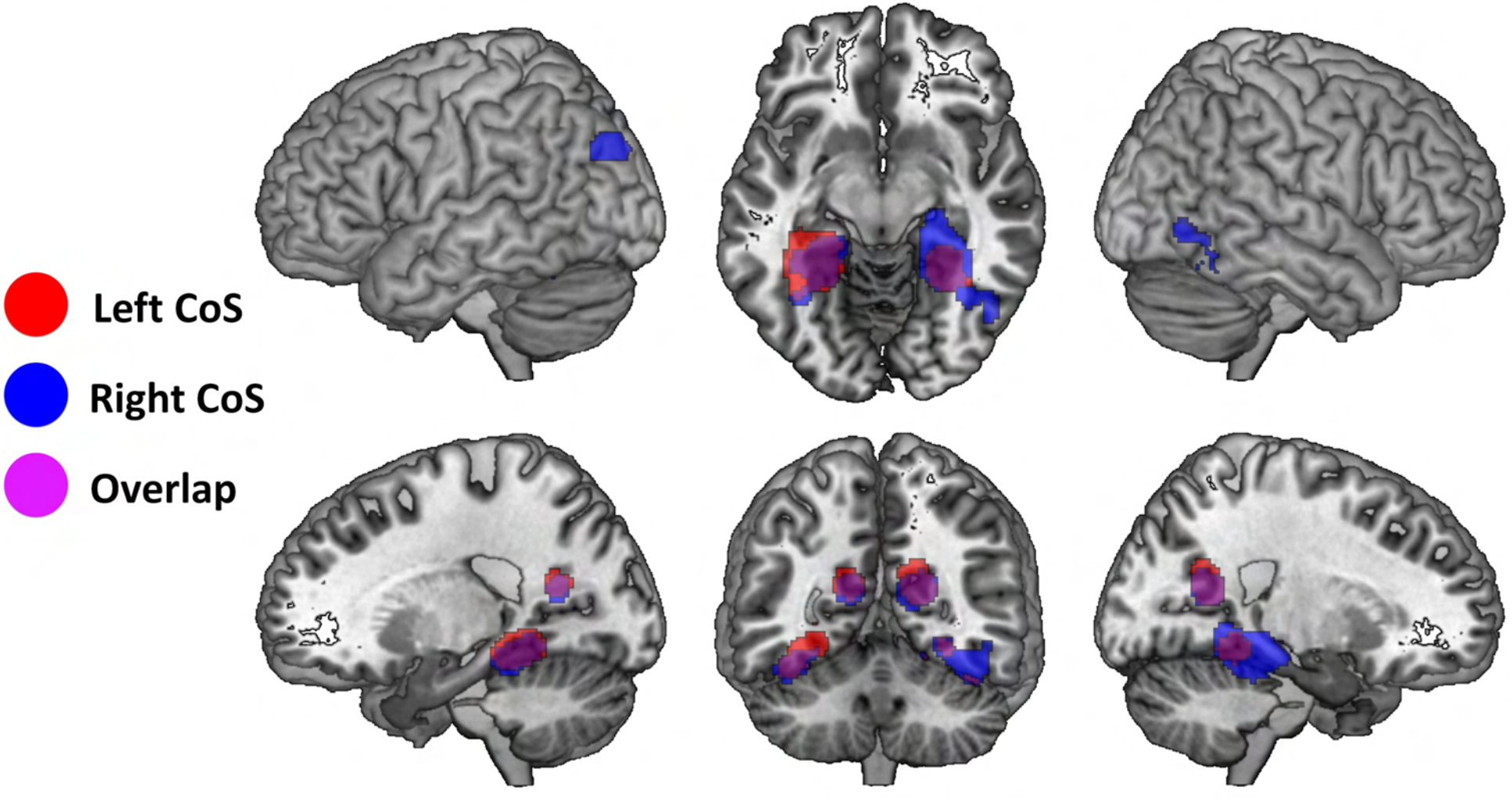
Fig. 4B. Differences in functional connectivity of right posterior middle temporal gyrus (pMTG) and right collateral sulcus (CoS) across both task-free and task-constrained states.

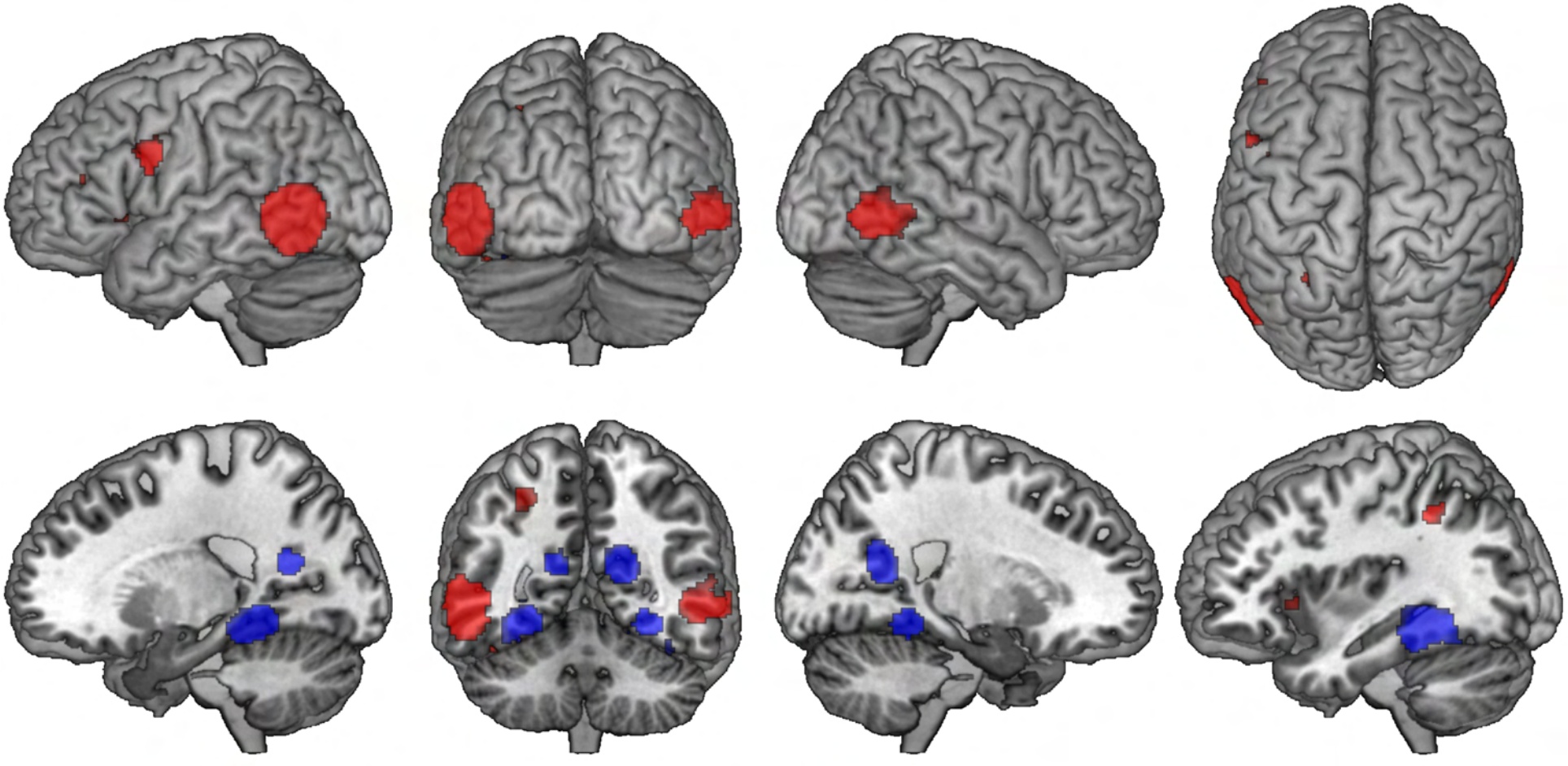
Fig. 5. Overlap in functional connectivity of right posterior middle temporal gyrus (pMTG) and collateral sulcus (CoS) across both task-free and task-constrained states.

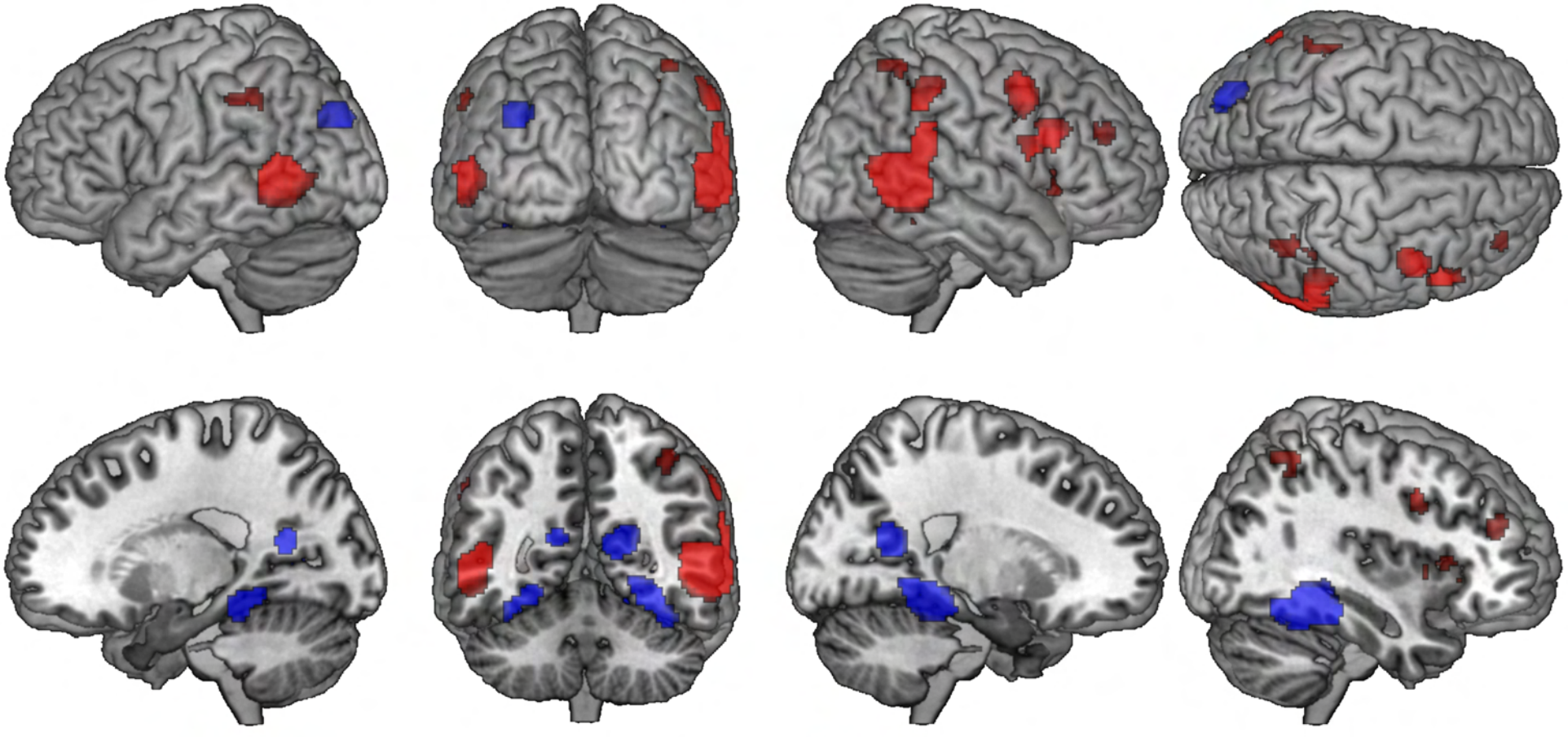
Fig. 6. Overlap in resting-state functional connectivity (RSFC) of all 4 seed regions: bilateral posterior middle temporal gyrus and bilateral collateral sulcus.

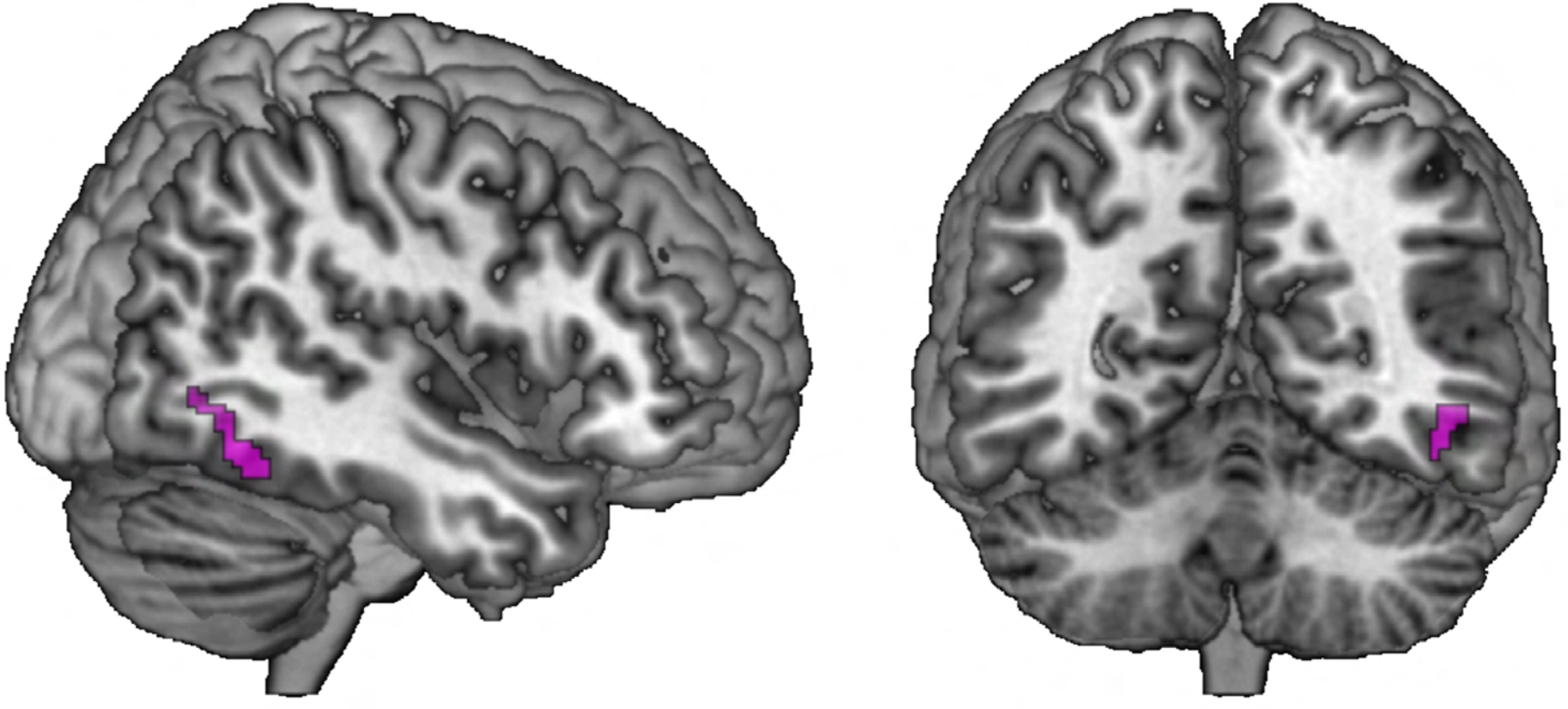

pMTG
CoS

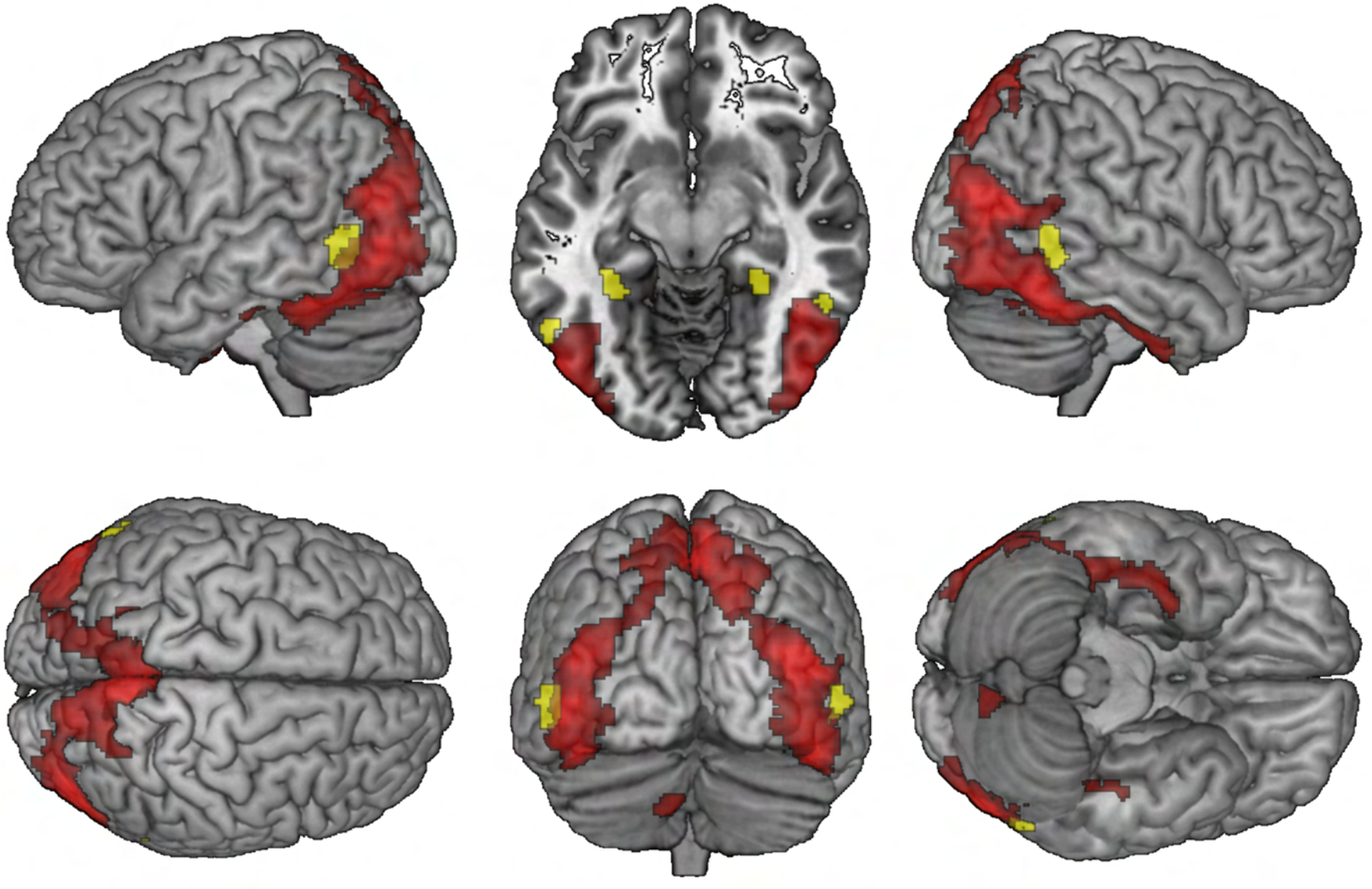

Left pMTG
Right pMTG
Overlap


Left CoS
Right CoS
Overlap


Left pMTG > Left CoS
Left CoS > Left pMTG


Right pMTG > Right CoS
Right CoS > Right pMTG




Seed Regions
RSFC Network Overlap

Supplementary Online Material

for

"A network view on brain regions involved in experts' object and pattern recognition: Implications for the neural mechanisms of skilled visual perception"

by

R. Langner, S.B. Eickhoff & M. Bilalić

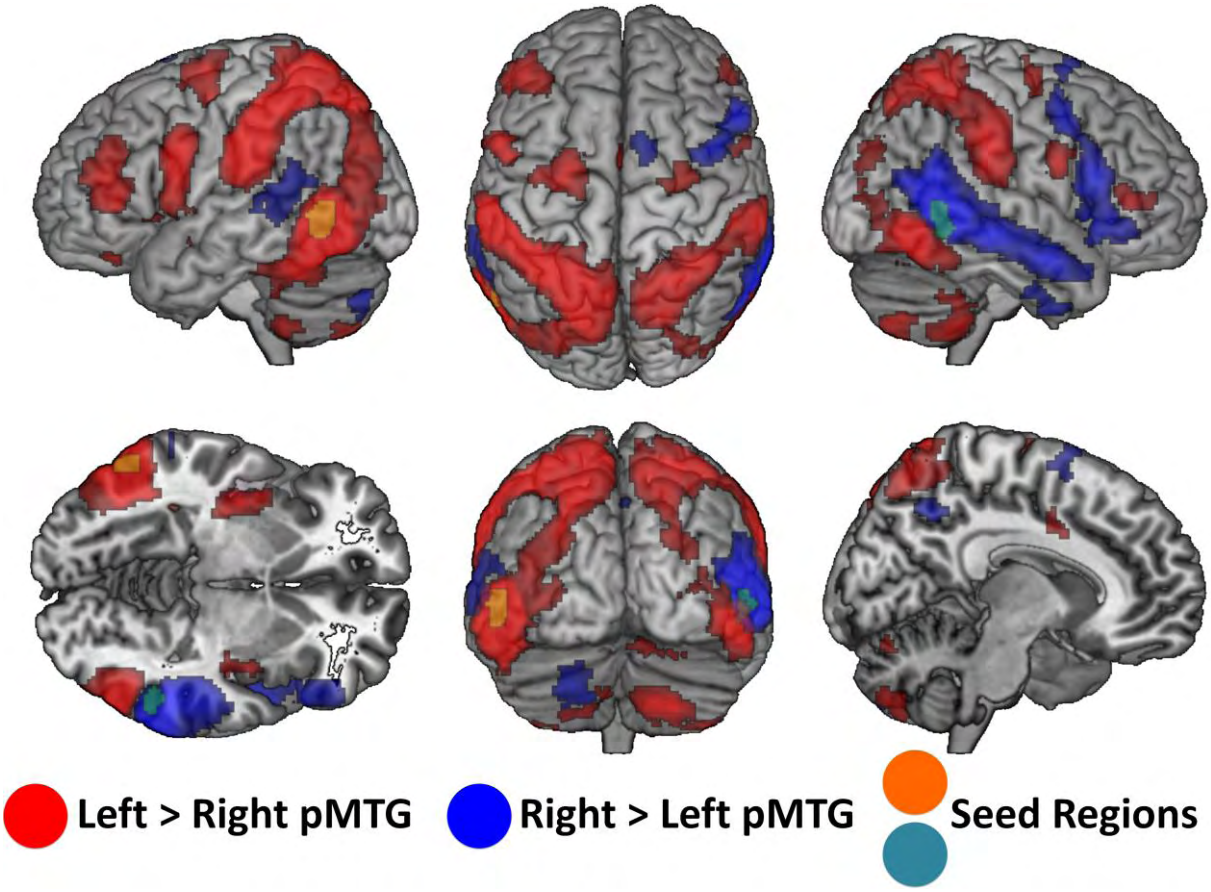


Figure S1. Differences in resting-state functional connectivity of right and left posterior middle temporal gyrus (pMTG).

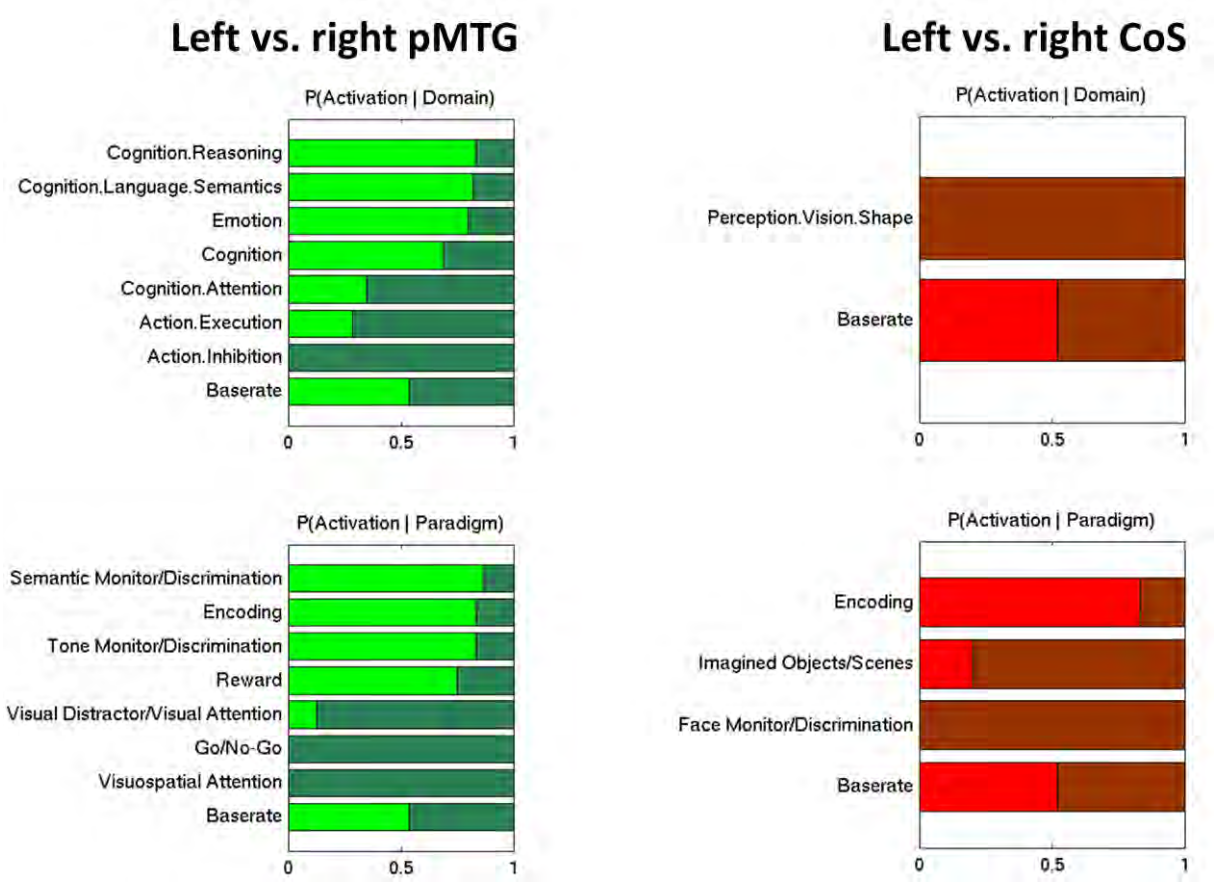


Figure S2. Differences in functional profiles (behavioural domains [upper panels] and paradigm classes [lower panels]) between left (light-green) and right (dark-green) posterior middle temporal gyrus (pMTG; left panels) as well as left (red) and right (brown-red) collateral sulcus (CoS; right panels). Baserate indicates distribution of experiments activating the left versus right seed region.

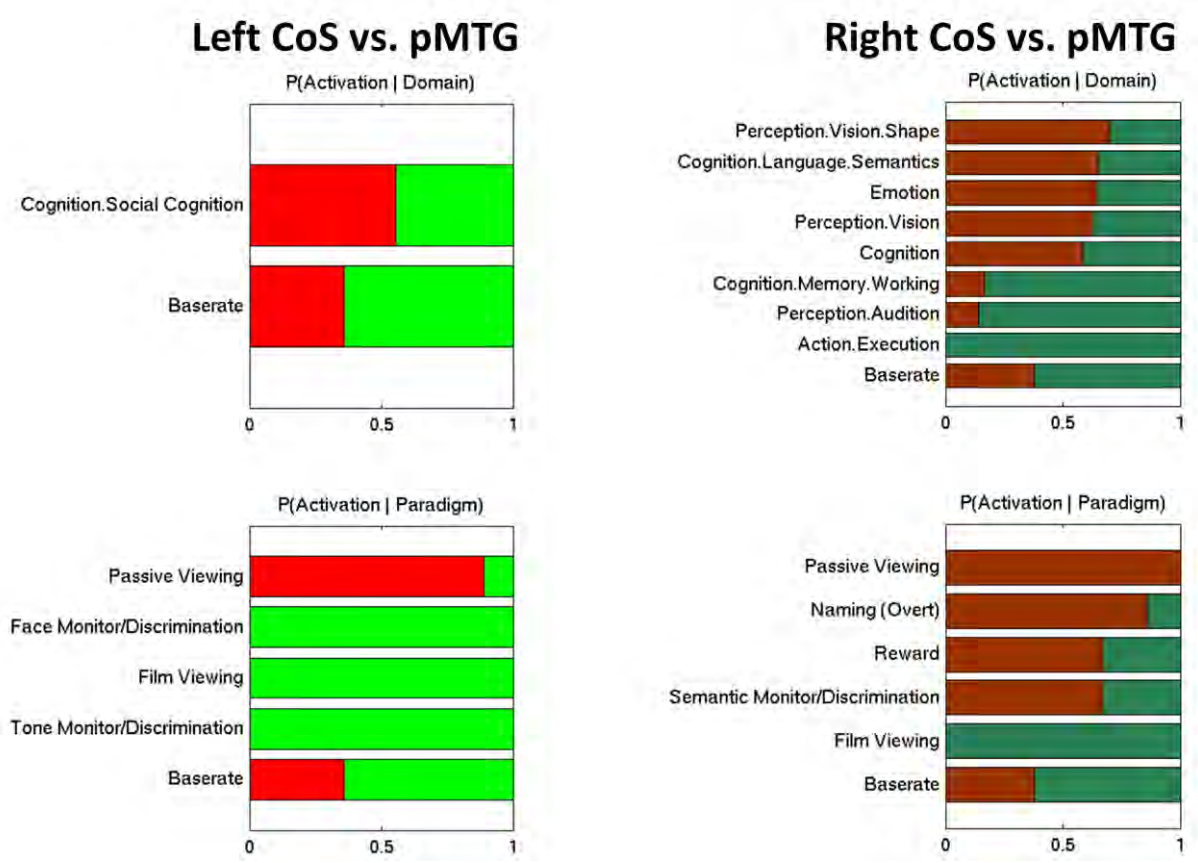


Figure S3. Differences in functional profiles (behavioural domains [upper panels] and paradigm classes [lower panels]) between collateral sulcus (CoS; red colours) and posterior middle temporal gyrus (pMTG; green colours). Baserate indicates distribution of experiments activating the CoS versus pMTG (per hemisphere).