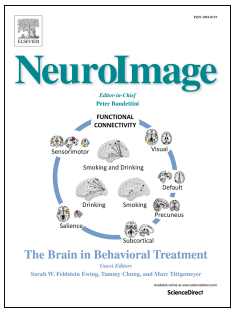
Accepted Manuscript



Oscillatory networks of high-level mental alignment: A perspective-taking MEG study

R.A. Seymour, H. Wang, G. Rippon, K. Kessler

PII: S1053-8119(18)30414-2

DOI: 10.1016/j.neuroimage.2018.05.016

Reference: YNIMG 14941

To appear in: *NeuroImage*

Received Date: 23 February 2018

Revised Date: 16 April 2018

Accepted Date: 4 May 2018

Please cite this article as: Seymour, R.A., Wang, H., Rippon, G., Kessler, K., Oscillatory networks of high-level mental alignment: A perspective-taking MEG study, *NeuroImage* (2018), doi: 10.1016/j.neuroimage.2018.05.016.

Oscillatory Networks of High-Level Mental Alignment: A Perspective-Taking MEG Study

Seymour, R.A[1,2,3]., Wang, H[1]., Rippon, G[1]., & Kessler, K[1].

[1]Aston Brain Centre, School of Life and Health Sciences, Aston University, Birmingham, B4 7ET. [2]ARC Centre of Excellence in Cognition and Its Disorders, Macquarie University, Sydney, Australia, 2109. [3]Department of Cognitive Science, Macquarie University, Sydney, Australia, 2109.

Correspondence: Klaus Kessler (k.kessler@aston.ac.uk)

School of Life and Health Sciences

Psychology, Aston Brain Centre

Aston University

Aston Triangle

Birmingham, B4 7ET

Phone: +44 (0)121 204 3187

19

Highlights

- Oscillatory basis of embodied perspective-taking investigated using MEG
- We replicate the crucial role of theta-band (3-6Hz) oscillations in perspective-taking
- Theta power localised to right temporo-parietal junction (rTPJ), lateral PFC and ACC
- Lateral PFC and ACC exert top-down influence (Granger causality) over rTPJ
- rTPJ increases its theta-band phase coupling to mentalizing and body schema networks

Abstract

Mentally imagining another's perspective is a high-level social process, reliant on manipulating internal representations of the self in an embodied manner. Recently Wang et al. (2016) showed that theta-band (3-7Hz) brain oscillations within the right temporo-parietal junction (rTPJ) and brain regions coding for motor/body schema contribute to the process of perspective-taking. Using a similar paradigm, we set out to unravel the extended functional brain network in detail. Increasing the angle between self and other perspective was accompanied by longer reaction times and increases in theta power within rTPJ, right lateral pre-frontal cortex (PFC) and right anterior cingulate cortex (ACC). Using Granger-causality, we showed that lateral PFC and ACC exert top-down influence over rTPJ, indicative of executive control processes required for managing conflicts between self and other perspectives. Finally, we quantified patterns of whole-brain phase coupling in relation to the rTPJ. Results suggest that rTPJ increases its theta-band phase synchrony with brain regions involved in mentalizing and regions coding for motor/body schema; whilst decreasing synchrony to visual regions. Implications for neurocognitive models are discussed, and it is proposed that rTPJ acts as a 'hub' to route bottom-up visual information to internal representations of the self during perspective-taking, co-ordinated by theta-band oscillations.

Keywords

perspective taking; social cognition; MEG; theta; oscillations; synchrony.

Introduction

Humans possess highly developed social skills that allow us to imagine what others might be experiencing, thinking or feeling to an extent not shared by other species (Tomasello et al. 2005). The question of what separates us from other species has been the subject of substantial research in comparative psychology and cognitive neuroscience, and while significant headway has been made with respect to what skills make us special (Call and Tomasello 1999; Povinelli et al. 2000; Frith and Frith 2007) and which parts of our brain have evolved to cope with sophisticated "mentalizing", i.e., reading of others' minds (Lieberman 2007; Van Overwalle and Baetens 2009), much less is known about the actual brain network dynamics that implement these social skills. Here we set out to investigate the large-scale, distributed but synchronised neural activity that gives rise to a person's understanding of another's visuospatial experience of the world: a process termed perspective taking.

Mentally imagining another's perspective is a high-level social process, but recent behavioural experiments suggest that perspective-taking is still grounded in the cortical posture and action representations of the observer. Using posture manipulations, several studies (Kessler and Rutherford 2010; Kessler and Thomson 2010; Surtees et al. 2013; Wang et al. 2016; Gooding-Williams et al. 2017) have shown that perspective-taking engages large parts of the neuronal bases of the body schema, i.e. the cortical correlates of the internal representation of the body (Coslett et al. 2008; Medina et al. 2009), in the form of a simulated rotation of the embodied self into another's orientation and perspective (Kessler and

Thomson 2010; Surtees et al. 2013; Wang et al. 2016). In other words, humans literally "put themselves" into another's viewpoint to understand their perspective.

Note that such embodied perspective-taking must be distinguished from so-called perspective *tracking*. While both processes involve judgements about another's perspective, perspective-tracking, in contrast to perspective-taking, merely requires an observer to understand what another can or cannot perceive (e.g. what is occluded and what is visible to them). The two forms of perspective processing have been related to different developmental stages (Flavell et al. 1981; Gzesh and Surber 1985; Moll and Tomasello 2006) (perspective-tracking: ~2 years; perspective-taking ~ 4-5 years) and perspective-tracking, in contrast to perspective-taking, has been observed in other species such as apes and corvids (Bugnyar et al. 2004; Bräuer et al. 2007). Finally, while perspective-taking engages an embodied mental rotation of the self into another's viewpoint, perspective-tracking seems to rely on inferring another's line of sight, in other words, whether their line of sight towards a target is disrupted or not (Zacks and Michelon 2005; Kessler and Rutherford 2010; Wang et al. 2016).

The neural correlates of embodied simulation during perspective-taking were recently investigated by Wang et al. (2016) using Magnetoencephalography (MEG, Expt. 1) and converging effects were found in the right posterior temporo-parietal junction (pTPJ) for cognitive effort of perspective-taking (amount of angular disparity between self vs. other's viewpoint) and for embodied processing (posture congruence) during perspective-taking (but not for tracking). The crucial role of right pTPJ for perspective-taking was further confirmed via transcranial magnetic stimulation (TMS) interference (Wang et al. 2016). The authors further reported that low frequency theta oscillations (3-7 Hz) were the prominent neural

code in pTPJ, whilst Gooding-Williams et al. (2017) used repetitive TMS entrainment over pTPJ to show that TMS pulses administered at theta frequency (6Hz) accelerated perspective-taking, while alpha (10Hz) entrainment slowed perspective-taking down. TPJ-theta could therefore be the relevant neural frequency to enable phase-coupling within a wider mentalizing network.

These results build upon a perspective-taking EEG study which found an evoked component at 450ms, localised primarily to the right TPJ (McCleery et al. 2011). Furthermore, they are consistent with the neural correlates of perspective-taking reported using fMRI – two meta-analyses (Van Overwalle 2009, 2011) have suggested that the core areas of activation include bilateral TPJ and ventro-medial pre-frontal cortex (vmPFC). The posterior division of the TPJ (Igelström and Graziano 2014; Bzdok et al. 2013) in particular, has been reliably linked to perspective-taking and more generally to “mentalizing” (representing other’s mental states) (Van Overwalle 2011; Schurz et al. 2013), as well as to so-called spontaneous “out-of-body experiences” (OBE) (Blanke et al. 2005). During an OBE individuals experience the sensation that the self has moved to a different physical location than their body, and this sensation often entails a translation as well as a rotation of perspective, similar to a deliberate perspective transformation during perspective-taking (Kessler and Braithwaite 2016). The involvement of TPJ in OBEs (Blanke et al. 2005) is of importance, as it corroborates the proposed link between embodied processing and high-level social mentalizing in TPJ (Blanke et al. 2005; Lombardo et al. 2010; Kessler and Braithwaite 2016; Wang et al. 2016).

Whilst the TPJ is clearly important for embodied processing and perspective-taking, the region is also implicated in a range of cognitive operations, including spatial attention, social cognition and self/other distinctions. It has been suggested that more generally, the region

acts as a major hub for information integration (Igelström and Graziano 2017.; Eddy 2016), especially during higher-level cognitive processes relying upon internal representations, such as perspective-taking (Igelström and Graziano 2017.; Eddy 2016; Wang et al. 2016; Gooding-Williams et al. 2017). Indeed, the TPJ has extensive functional connectivity to many networks of the brain, including the fronto-parietal control (Vincent et al. 2008), default mode (Mars et al. 2012), and ventral attention networks (Bzdok et al. 2013). We therefore hypothesised that the TPJ contributes to the process of embodied transformation through changes in patterns of whole-brain functional connectivity, via theta-band synchrony, as would be predicted from the region's role as a network hub (Igelström and Graziano 2017.; Carter and Huettel 2013; Eddy 2016). However, investigations of perspective-taking using connectivity analysis, e.g. in form of frequency-specific phase-coupling, are scarce. To our knowledge, only one study to date (Bögels et al. 2015) has reported enhanced theta phase-coherence between right TPJ and ventromedial prefrontal cortex (vmPFC) in a condition that required participants to imagine another's visual experience. The major aim of the current study was therefore to consolidate the crucial role of pTPJ theta oscillations in perspective-taking by means of advanced network analyses.

In addition to the TPJ, Wang et al., reported increases in theta-band power for the lateral PFC during the cognitive effort of perspective-taking (Wang et al. 2016). Activity within this region during social cognition has been argued to reflect high-level reasoning and working memory processes recruited more generally during complex perspective-taking and mentalizing tasks (Van Overwalle 2011). However, there is emerging evidence that frontal activity in lateral PFC but also in the anterior cingulate cortex (ACC) could play a more nuanced role in perspective-taking by managing the conflict between self and other perspectives (Samson et al. 2005; Bögels et al. 2015; Hartwright et al. 2015). For example

(McCleery et al. 2011) found late a (0.8-1.0s) frontal evoked response during perspective-taking dependent on whether self perspective was consistent with an avatar's perspective . In terms of theta-oscillations, this could potentially manifest as a direct connection between lateral PFC and the core mentalizing network (Bögels et al. 2015) in TPJ and vmPFC (Van Overwalle 2009, 2011). We were therefore interested in whether the TPJ becomes functionally connected to various frontal and midline regions during perspective-taking (Hartwright et al. 2015), and crucially determining the direction of this connectivity.

In conclusion, we set out to consolidate previous findings regarding the crucial role of TPJ theta oscillations for generating the abstract social representations required for perspective-taking (Bögels et al. 2015; Wang et al. 2016; Gooding-Williams et al. 2017), while unravelling in detail the involved functional network in terms of dynamic oscillatory coupling between brain areas, using MEG. Based on the considerations above, we expected TPJ and (v)mPFC to form a mentalizing network synchronised via theta oscillations, related to generating the abstract representation of another's perspective, while activation in parietal body-schema areas and sensorimotor cortex would reflect the required embodied transformation to generate this representation via rotation of the egocentric perspective (Kessler and Rutherford 2010; Kessler and Thomson 2010; Surtees et al. 2013). In addition, pACC and lPFC might play key roles in top-down executive control of the underlying embodied transformation and in managing the conflict between physical self and transformed self at the representational level.

Materials and Methods

Participants

Data were collected from 18 participants (4 male, 14 female, mean age = 27.55, SD = 5.86). All participants had normal or corrected to normal vision and no history of neurological or psychiatric illness. All experimental procedures complied with the Declaration of Helsinki and were approved by the Aston University, Department of Life & Health Sciences ethics committee. Written consent was obtained from all participants.

Experimental Paradigm and Design

The paradigm was adopted from a behavioural study by Kessler and Rutherford (2010). The stimuli were coloured photographs (resolution of 1024 × 768 pixels), showing an avatar seated at a round table shown from one of four possible angular disparities (see Fig. 1, left: 60°, 160° clockwise and anticlockwise). In each trial one of the grey spheres on the table turned red indicating this sphere as the target. From the avatar's viewpoint, the target could be either visible or occluded (VO) by a centrally resented black screen; or to the left or to the right (LR) inducing perspective-tracking or perspective-taking, respectively. Stimuli were presented in 12 mini-blocks of 32 trials, alternating between LR and VO conditions. On each trial participants were asked to make a target location judgement according to the avatar's perspective by pressing the instructed key on an MEG-compatible response pad: the left key for “left” or “visible” targets from the avatar’s viewpoint and the right key for “right” or “occluded” targets. Accuracy feedback was provided after each trial in the form of a short tone. As in Kessler and Rutherford (2010), we collapsed across clockwise and anticlockwise disparities, and separately collapsed correct responses for left and right and visible and occluded, respectively. This resulted in four separate experimental conditions (for two examples see Fig. 1, left): left/right judgements where the avatar is 160^0 from own perspective (LR-160); left-/right judgements where the avatar is 60^0 from own perspective (LR-60); visible/occluded judgments where the avatar is 160^0 from own perspective (VO-

160); visible/occluded judgments where the avatar is 60^0 from own perspective (VO-60). This 2x2 design allowed us to disentangle perspective-taking from perspective-tracking and investigate the effect of an increased angle of disparity (we chose to use 160° vs. 60° based on the results of Wang et al., 2016), between self-perspective and other-perspective, which has been shown to lengthen reaction times during perspective-taking (Kessler and Rutherford 2010; Surtees et al. 2013).

Behavioural Data Analysis

Behavioural reaction times (RT) from the experimental paradigm were extracted from E-Prime® data files and converted to *.csv* format. Data from two participants with MEG movement over 5mm was discarded. All trials containing incorrect answers or response times greater than 2 standard deviations from the median were excluded from subsequent analyses. For the four experimental conditions (LR-160; LR-60; VO-160; VO-60), median RT from each participant were entered into a one-way ANOVA using the JASP statistics package.

MEG and Structural MRI Acquisition

MEG data were acquired using a 306-channel Neuromag MEG scanner (Vectorview, Elekta, Finland) made up of 102 triplets of two orthogonal planar gradiometers and one magnetometer. All recordings were performed inside a magnetically shielded room at a sampling rate of 1000Hz. Five head position indicator (HPI) coils were applied for continuous head position tracking, and visualised post-acquisition using an in-house Matlab script. Two participants had excessive head movement (>5mm), and were excluded from subsequent analyses. For MEG-MRI coregistration purposes three fiducial points, the locations of the HPI coils and 300-500 points from the head surface were acquired using the integrated Polhemus Fastrak digitizer. Visual stimuli were presented on a projection screen

located 86cm from participants, and auditory feedback through MEG-compatible headphones. Data acquisition was broken down into three sequential runs, each lasting 8-10 minutes.

A structural T1 brain scan was acquired for source reconstruction using a Siemens MAGNETOM Trio 3T scanner with a 32-channel head coil (TE=2.18ms, TR=2300ms, TI=1100ms, flip angle=9°, 192 or 208 slices depending on head size, voxel-size = 0.8x0.8x0.8cm).

MEG Preprocessing

All MEG data were pre-processed using Maxfilter (temporal signal space separation, .96 correlation), which supresses external sources of noise from outside the head (Taulu and Simola 2006). To compensate for head movement between runs, data from runs 2 and 3 were transformed to participant's head position at the start of the first block using the *–trans* option of Maxfilter. For each participant, the entire recording was band-pass filtered between 0.5-250Hz (Butterworth filter) and band-stop filtered to remove residual 50Hz power-line contamination and its harmonics. Data were then epoched into segments of 2500ms (1000ms pre, 1500post stimulus onset) and each trial was demeaned and detrended. Trials containing artefacts (SQUID jumps, eye-blinks, head movement) were removed by visual inspection, resulting in removal of an average of 6.14% of trials per condition, per participant (additional descriptive statistics reported in Table S1). For sensor-level analyses, ICA was used to identify and reduce residual EOG and ECG artefacts. Four MEG channels containing large amounts of non-physiological noise were removed from all source-level analyses. The pre-processed data were then separated into the four experimental conditions and downsampled to 250Hz to aid computation time.

MEG-MRI Coregistration

MEG data were co-registered with participants' T1 MRI structural scan by matching the digitised head shape data with surface data from the structural scan (Jenkinson and Smith 2001). Subsequently, the aligned MRI-MEG image was used to create (i) a forward model based on a single-shell description of the inner surface of the skull (Nolte 2003), using the segmentation function in SPM8 and (ii) spatial normalisation parameters to create individual volumetric grids. To facilitate group analysis, each individual volumetric grid was warped to a template based on the MNI brain (8mm resolution). Subsequently the inverse of the normalisation parameters were applied to the template grid, for source analysis.

Sensor Level Analysis

Sensor-level time-frequency representations (TFRs) were calculated using a single Hanning taper between frequencies of 1-30Hz in steps of 1Hz. The entire 2500ms epoch was used, with a sliding window of 500ms, but the first 250ms and last 500ms of each trial were discarded to avoid edge artefacts. Due to different scales between the two MEG sensor-types, only data from the gradiometers were used, with TFR power averaged across each pair post-hoc. All analyses were computed on single trials and subsequently averaged, and therefore TFRs contain both phase-locked (evoked) and non phase-locked (induced) information. As hypothesised from previous research using a similar paradigm (Wang et al. 2016), TFR responses averaged across subjects showed prominent differences between conditions within the theta-band (2-7Hz).

For statistical testing, we therefore compared theta-band (2-7Hz), alpha (8-12Hz) and beta (13-30Hz) power during trials in which the avatar was 160^0 versus 60^0 from the participant's

own perspective (clockwise or anticlockwise), in both left/right judgements (i.e. perspective-taking), and visible/occluded judgements (i.e. perspective-tracking). We corrected for multiple comparisons across time, frequency and space via cluster-based non-parametric permutation testing (Maris and Oostenveld 2007). Results showed a significant cluster of greater (3-6Hz) theta-band power at 0-650ms in the LR-160 versus LR-60 condition (highlighted in Fig S1, left), but not for VO-160 vs. VO-60, (Fig. S1, right).

MEG Source-Level

Source localisation was conducted using Dynamical Imaging of Coherent Sources (Gross et al. 2001) (DICS) which applies a spatial filter to the MEG data at every voxel of a canonical 0.8 cm brain-grid, in order to maximise signal from that location whilst attenuating signals elsewhere. The spatial filter was calculated from the cross-spectral densities for a time–frequency tile centred on the effects found at sensor level (3-6Hz; 0–650ms; gradiometer channels only; see Fig. 1, top-right; Supplementary Figure S1). For all analyses, a common filter across baseline and active periods was used and a regularisation parameter of lambda 5% was applied. Cluster-based non-parametric permutation testing was used to correct for multiple comparisons across voxels (Maris and Oostenveld 2007), for the LR-160>LR-60 and VO-160>VO-60 contrasts. The resulting whole-brain statistical maps were spatially smoothed using a robust smoothing algorithm (Garcia 2010) as implemented in bspmview, and presented on a 3D cortical mesh using the Connectome Workbench software (Van Essen et al. 2012). Using the spatial filters computed during source analysis, we extracted trial-by-trial time-courses from three regions of interest, as shown in Fig. 2A, using the MNI co-ordinates with the highest t-value within each region (Table S3).

Granger Causality Analysis

The directed functional connectivity between these three ROIs was estimated using spectrally-resolved non-parametric Granger causality (Dhamala et al. 2008) as implemented in the Fieldtrip toolbox (Oostenveld et al. 2010). Intact and scrambled time-series were split into 0.325s epochs to enhance the accuracy of the results (0-0.65s post stimulus onset), followed by Fourier transformation (Hanning taper; 2Hz spectral smoothing), before being entered into a non-parametric spectral matrix factorisation procedure. Granger causality was then estimated between each ROI pair and each ROI-scrambled time-series. Statistical analysis was performed using cluster-based permutation testing (Maris and Oostenveld 2007). Granger causal influence between two regions (A & B) was deemed significant if values were i) significantly greater than scrambled data ($p<.05$) and ii) significantly greater in one direction than another (i.e. A-to-B versus B-to-A, $p<.05$).

Theta-band Imaginary Coherence

To estimate patterns of whole-brain connectivity supporting high-level perspective taking, mediated by the right TPJ, we quantified theta-band phase synchrony during LR-160 trials compared with LR-60 trials. A complex-valued spectral estimate at 5±2Hz for each grid-point was estimated using an adaptive spatial filter [the 'PCC' method, as implemented in *ft_sourceanalysis* (Oostenveld et al. 2010)]. Coherence was used to quantify the phase consistency between a seed region in TPJ (MNI co-ordinates [40 -58 36]) and every other voxel of the canonical 0.8 cm brain-grid, using *ft_connectivityanalysis* (Oostenveld et al. 2010). Coherence values are normalised to range from 0 (no phase synchrony) to 1 (completely phase synchronised). We opted to project the complex-valued coherency estimates onto the imaginary axis, as suggested by Nolte et al., (Nolte et al. 2004). This removes estimates of instantaneous phase, thereby reducing the influence of spurious connectivity resulting from MEG field spread (Nolte et al. 2004), but comes at the expense of

removing genuine connectivity at zero-lag. Further details on the quantification of "imaginary coherence" can be found elsewhere (Nolte et al. 2004; Oostenveld et al. 2010). Whole-brain coherence maps from LR-160 and LR-60 trials were baseline-corrected and compared using cluster-based permutation-testing as implemented in the Fieldtrip toolbox (Oostenveld et al. 2010). The resulting whole-brain statistical maps were spatially smoothed using a robust smoothing algorithm (Garcia 2010) as implemented in bspmview, and presented on a 3D cortical mesh using the Connectome Workbench software (Van Essen et al. 2012).

Supplementary Methods and Analysis Code

Additional details are provided in SI Materials and Methods. MATLAB code for all analyses is openly available online at https://github.com/neurofractal/perspective_taking_oscillatory_networks (Seymour 2017).

Results

Behavioural Results

For the four experimental conditions, median reaction times (RT) from each participant were entered into a one-way ANOVA (output detailed in Table S2). Results showed a main effect of experimental condition on RT, $F(3,60) = 4.43$, $p=.007$, $\eta^2 = 0.181$. Post-hoc tests revealed this was due to significantly longer RT for the LR-160 conditions compared with all other conditions (LR-60, $p_{tukey}= .013$; VO-160, $p_{tukey}= .029$; VO-60, $p_{tukey}= .026$), replicating Kessler and Rutherford (2010). The raw statistical output is reported in Table S2.

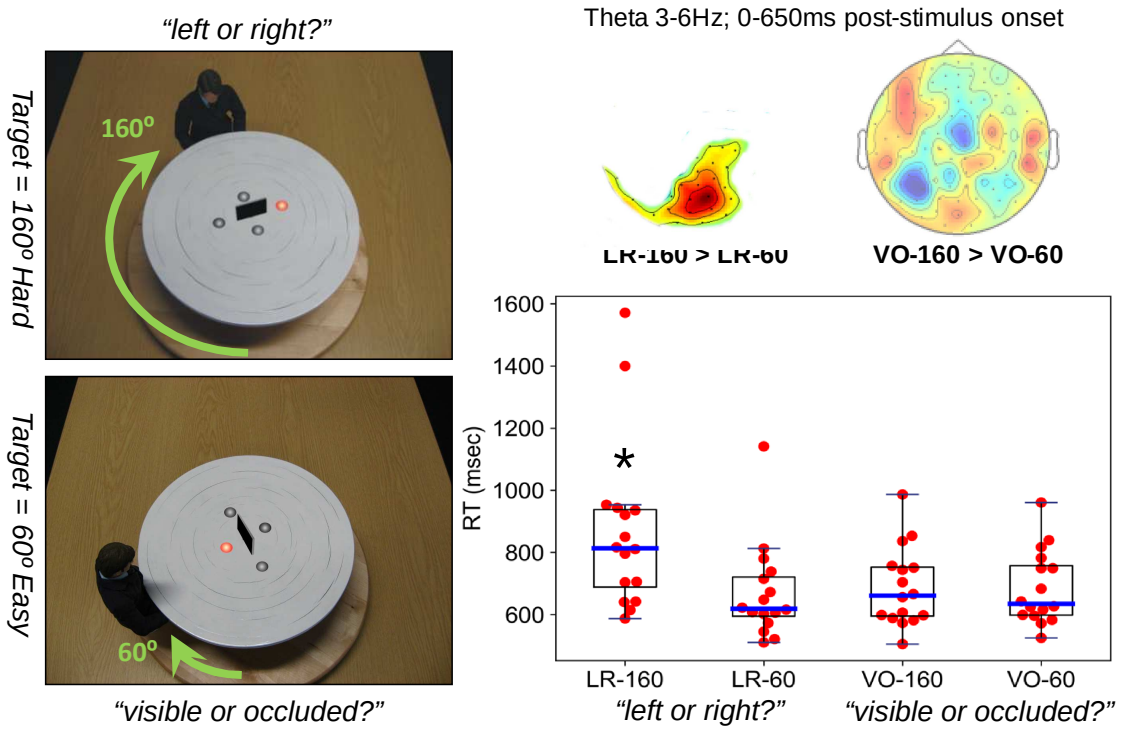


Figure 1. Left: Experimental paradigm (Kessler and Rutherford 2010) showing two example stimuli (see Materials and Methods for details). Bottom right: Boxplot of participants' (N = 16, 2 participants removed with excess head movement) median reaction time (RT) in milliseconds for the two angular disparity conditions (160 vs. 60) of perspective-taking (L/R) and perspective-tracking (V/O), respectively. * = LR-160 is significantly different from all other conditions (p<.05). Top right: Sensor-level topoplots of theta activity (3-6Hz), showing a significant cluster (high visibility) for perspective-taking but not for perspective-tracking (further details in Materials and Methods and supplementary information).

Task-Related Changes in Theta Power

Using a data-driven approach from 2-30Hz, time-frequency results at the sensor-level (see Fig. 1 and Fig. S1) replicated the crucial role of theta oscillations in perspective-taking (Wang et al. 2016; Gooding-Williams et al. 2017). A significant positive cluster (p=0.03) was found at 3-6Hz, 0-650ms, when comparing angular disparities of 160° and 60° degrees for

the L/R task. No significant effects were found for any other frequencies (p>.05). In addition, no significant clusters were found for the V/O task, i.e. perspective-tracking in the VO-160 vs VO-60 contrast.

[Inline supplementary material - Insert Figure S1 here]

Based on these sensor-level data, which replicate our previous study (Wang et al., 2016), we decided to concentrate on further characterising theta-band power and connectivity underlying perspective-taking. Whilst a wider frequency range, that also included higher delta frequencies, has been used to define theta-band power in previous studies (Wang et al. 2016), we opted to use 3-6Hz, based on the statistical analysis of the sensor-level data in order to achieve the best signal-to-noise ratio for subsequent beamforming analyses.

To investigate the cortical sources underlying this effect of angular disparity, theta-band (3-6Hz) power was localised from 0-650ms post-stimulus onset separately for 160° and 60° trials, using the Dynamic Imaging of Coherent Sources (DICS) approach (see Materials and Methods). Baseline-corrected theta (3-6Hz) power was compared for LR-160 versus LR-60 trials and VO-160 versus VO-60 trials across a 0.8cm cortical grid (Fig. 2A; Supplementary Table S3). Results showed a significant (Maris and Oostenveld 2007) (p<.05) increase in theta power during LR-160 trials compared with LR-60 trials for right posterior temporo-parietal junction (pTPJ) spreading into the inter-parietal sulcus (IPS), for right lateral pre-frontal cortex (PFC) primarily overlapping with the inferior frontal gyrus (IFG) and for right anterior cingulate cortex (ACC). There was also a decrease in theta power in the LR-160 versus LR-60 condition in the left frontal pole (Table S3).

For perspective-tracking (VO-task), there were increases in theta-power, compared with pre-trial baseline, within ventral occipital and temporo-parietal regions (Fig. S2). However, the VO-160 > VO-60 contrast showed no significant clusters (Fig. S3), indicating that angular disparity (160° versus 60°) only resulted in task-related increases in theta-band power for high-level perspective-taking and not for perspective-tracking.

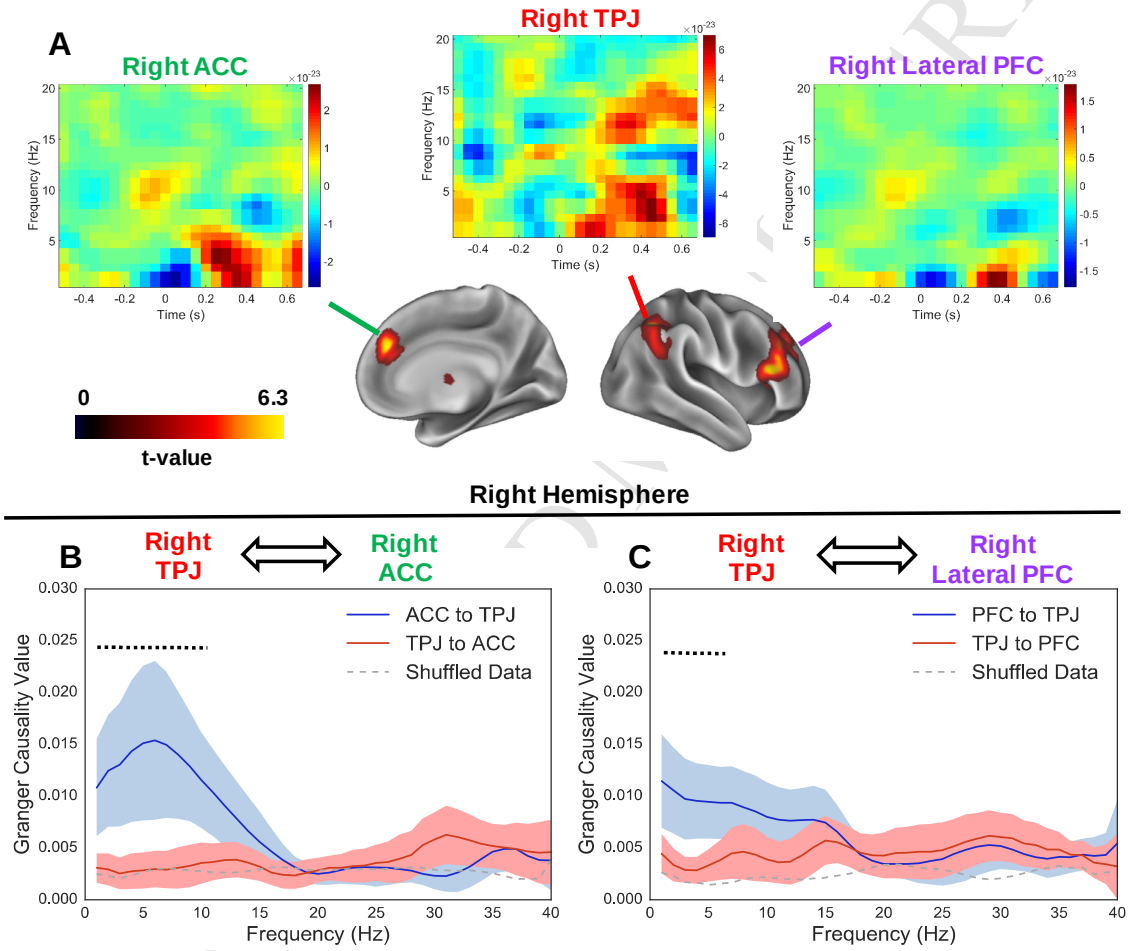


Figure 2: Theta power sources and directed connectivity. Panel A depicts brain plots showing statistical results (clusters with p<.05 are shown) of a whole-brain DICS theta power (3-6Hz) analysis for LR-160 > LR-60 contrast visualised using the Connectome Workbench software (Van Essen et al. 2012) (see Table S3 for a complete list of power sources). Plots at the top show time-frequency representations (LR-160 > LR-60 contrast) for three virtual

electrodes (VE) placed in right ACC (MNI co-ordinates: [12, 36, 28]), right TPJ (MNI co-ordinates [40 -58 36]) and right lateral PFC (MNI co-ordinates: [52,32,16]). Panel B shows spectrally resolved non-parametric Granger causality (1-40Hz), computed between the right TPJ and (A) right ACC and (B) right lateral PFC, respectively. Results show an increase in Granger causality from both the right ACC (1-10Hz) and right PFC (1-5Hz) to the right TPJ. Shaded regions around each line represent 95% confidence intervals. The black dotted line above the plots represents Granger causality values passing a $p<.05$ threshold (see Methods for details). The grey dotted line in the plots shows shuffled data for comparison. Further explanations in the text.

[Inline supplementary material - insert Figures S2 and S3 here]

Virtual Electrode Time-Frequency Analysis

To further investigate the oscillatory signatures of high-level perspective-taking, time-courses for each trial were extracted from 'virtual-electrodes' in right TPJ, right ACC and right lateral PFC (see Materials & Methods for details). Low-frequency oscillatory power was then estimated between -0.65 to 0.65s post-stimulus using a Hanning taper, 0.05s sliding window. Results show very early and sustained theta power (3-6Hz) increases in the right TPJ (0-0.5s) for LR-160 versus LR-60 trials. Right lateral PFC delta/theta power (1-5Hz) and right ACC (1-5Hz) increases are more transient and begin from 0.2-0.5s post-stimulus onset. This suggests that the rTPJ is engaged throughout the process of embodied perspective-taking, whereas increases in theta power ACC and PFC occur later and more transiently.

Granger Causality Analysis

To investigate directed functional connectivity during perspective-taking between the three main regions of interest (ROIs) identified in the source power analysis (rTPJ, rACC and rPFC), we employed spectrally resolved non-parametric Granger causality (GC) on LR trials (0-0.65s post-stimulus onset) (Dhamala et al. 2008). GC is a statistical concept used to estimate directed connectivity between time-series, which relies on the premise that if the time-series of region *A* can be used to predicts the time-series of region *B*, then *A* is said to 'granger-cause' *B* (Ding Mingzhou et al. 2006). GC can also be extended to the frequency domain (discussed further in (Bastos and Schoffelen 2016). Spectrally-resolved GC therefore provides information about the direction of connectivity between regions of interest, as well as the frequency-band underlying the effects.

Between the three ROIs, GC values showed statistically significant differences from fourier-scrambled time-series in two pairs: rTPJ-rACC and rTPJ-rPFC (Maris and Oostenveld 2007). To investigate these effects further, we statistically compared GC values between each direction of the ROI pair (i.e. the granger causal influence to and from the rTPJ). Results showed an asymmetric increase in granger causal influence, directed from right ACC between 1-10Hz, with a peak at 6Hz, (Fig. 2B, p=.009) and right PFC, between 1-6Hz, (Fig 2B, p=.04) to the right TPJ.

Imaginary Coherence

Phase-synchronised neural activity has been argued to act as a mechanism for information flow between brain regions during cognitive tasks (Womelsdorf et al. 2007). Measures of phase synchrony (e.g. coherence) can therefore provide information about changes in brain connectivity within a particular frequency band. However unlike GC, coherency alone does not provide information about the direction of connectivity.

To establish patterns of whole-brain functional connectivity accompanying right-hemisphere TPJ theta-band activity, we extracted source-level theta-band (5±2 Hz) phase relationships from the sensor-level cross-spectral density matrix (see Materials and Methods). A measure of phase synchrony between a right-TPJ seed and every other voxel was calculated by projecting complex-valued coherency onto the imaginary axis (Nolte et al. 2004). The resulting coherency maps from the LR-160 and LR-60 conditions were first baseline-corrected, and then compared using cluster-based non-parametric permutation testing (Maris and Oostenveld 2007).

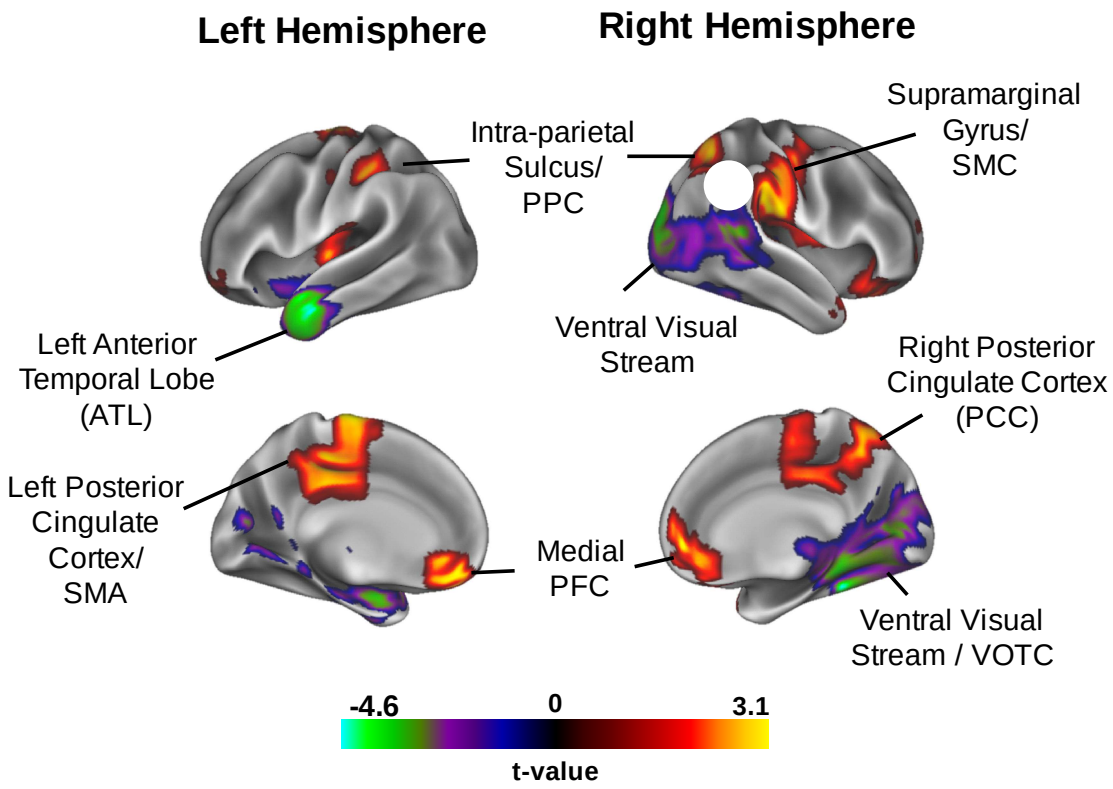


Figure 3: Results of a whole-brain imaginary coherence analysis in relation to a right TPJ seed (white circle) and for a LR-160 > LR-60 contrast, visualised using the Connectome Workbench software (Van Essen et al. 2012) (see Table S4 for a complete list of sources and

associated p-values). Clusters of coherency increase/decrease passing a p<.05 threshold are shown (see Material and Methods). PPC = posterior parietal cortex; SMC = sensorimotor cortex; SMA = supplementary motor area; PFC = prefrontal cortex; VOTC = ventral occipitotemporal cortex.

Results (Fig. 3) show a complex pattern of both increased and decreased theta-band phase synchrony during embodied perspective-taking. The main areas of decreased synchrony are located in the ventral occipitotemporal cortex (VOTC), overlapping with key regions of the ventral visual stream. There were also reductions in phase synchrony to the bilateral anterior temporal lobes (ATL). Increased phase synchrony was observed in bilateral medial PFC regions, posterior cingulate cortex (PCC), intra-parietal sulcus (IPS), supplementary motor area (SMA), posterior parietal cortex (PPC), and right supramarginal gyrus/sensorimotor cortex (SMC). These patterns of phase synchrony are unlikely to be driven by spurious connectivity from MEG field spread (Brookes et al. 2011), as we opted to measure imaginary coherence (Nolte et al. 2004), thereby removing effects in relation to instantaneous phase.

Discussion

This MEG study has investigated the oscillation-based functional connectivity between brain regions involved in our ability to take another person's visuospatial perspective. Behavioural results replicated a substantial body of research showing significantly increased reaction time for higher angular disparity between the participant and avatar (160° versus 60°) for perspective-taking but not perspective-*tracking* (Kessler and Rutherford 2010; Kessler and Thomson 2010; Surtees et al. 2013; Wang et al. 2016). Greater angular disparity for perspective-taking was accompanied by increased theta power (3-6Hz) within the right

TPJ/IPS and lateral PFC, replicating Wang et al., (Wang et al. 2016), as well as within the right ACC. Importantly, this increase in theta-power for angular disparity was specific to perspective-taking and not perspective-tracking (Figs. 1, S1, S3). We therefore focused on network connectivity during perspective-taking and showed (Fig. 2) that there was an increase in Granger causal influence (Dhamala et al. 2008) from lateral PFC and right ACC *to* right TPJ, but not vice-versa, mediated by low frequency brain rhythms (1-10Hz). Finally, we examined how whole-brain patterns of theta-band (5±2 Hz) phase synchrony, quantified using imaginary coherence (Nolte et al. 2004), varied in relation to right TPJ activity. Results (Fig. 3) suggest that with increasing angular disparity (160° versus 60°), the right TPJ increases its phase coupling to regions involved in theory of mind (Carrington and Bailey 2009) (medial PFC, PCC) and body schema (Coslett et al. 2008; Medina et al. 2009) (SMC, PPC, SMA), but decreases its phase coupling to visual regions (VOTC) and to bilateral anterior temporal lobe (ATL). Overall, these results suggest a crucial role for TPJ as a hub that functionally connects mentalizing, executive, and body-representational networks via theta-band (3-7Hz) oscillations during high-level perspective taking (Fig. 4).

The role of the right TPJ in high-level perspective-taking

Results from this study suggest that the right TPJ (rTPJ) becomes increasingly engaged with the need for embodied mental alignment during perspective-taking i.e. as the disparity grows between our own and other's perspectives (Wang et al. 2016; Gooding-Williams et al. 2017). Activity within the right TPJ is consistent with its role in establishing a sense of self (Blanke et al. 2005), and crucially in differentiating conflicts between the self and other (Santiesteban et al. 2012; Sowden and Catmur 2015; Eddy 2016). The left TPJ has also been implicated in theory of mind and perspective-taking tasks (Santiesteban et al. 2012; Schurz et al. 2013), however our results, replicating Wang et al., (2016) suggest that theta-band power is stronger

within the right TPJ, when there is a large angle of disparity (e.g. 160°) between self and other perspective is greatest. This is consistent with some findings of lateralisation in TPJ function (Igelström and Graziano 2017.). Given the importance of the rTPJ in perspective-taking (Santiesteban et al. 2012; Schurz et al. 2015; Eddy 2016; Wang et al. 2016), we were interested in further describing the neurocognitive processes involved.

As previous research has implicated the TPJ as a major network hub (Igelström and Graziano 2017.; Bzdok et al. 2013), we hypothesised that the region would co-ordinate shifts in functional connectivity to other brain regions, via phase synchrony (Engel et al. 2001; Varela et al. 2001). Indeed, we found that the rTPJ increased its phase-coupling to the medial PFC and posterior PCC – two regions also involved more generally in understanding the mental states of others (Lieberman 2007; Carrington and Bailey 2009; Van Overwalle 2009) (i.e. mentalizing). Importantly, phase-coupling at theta frequency between rTPJ and medial PFC had been previously reported by Bögels et al (2015) during a high-level mentalizing task. Thus, TPJ-mPFC coupling could be part of a basic mechanism involved in simpler as well as in more sophisticated forms of social mental alignment.

We also found increased phase synchrony between the rTPJ and SMC, SMA, and PPC (Fig. 3), regions previously implicated in coding for the body schema, i.e. cortical correlates of the internal representation of the body and its postures and actions (Coslett et al. 2008; Medina et al. 2009). We propose that this functional link, which has been reported previously (Arzy et al. 2006; Cazzato et al. 2015), underlies the simulated rotation of the embodied self into another's orientation and perspective, which so far has primarily been described behaviourally (Kessler and Rutherford 2010; Surtees et al. 2013; Wang et al. 2016). The rTPJ also showed decreased phase synchrony with visual regions (VOTC), primarily the ventral

stream of the right visual cortex, during high-level perspective-taking. Altogether, these findings can be interpreted as an active shift from externally-driven processing (i.e. bottom-up sensory information) to internal representations (i.e. self, body-schema rotation) during high level perspective-taking. This switch from processing external events to updating internal states and information has been previously linked with TPJ function (Bzdok et al. 2013; Wu et al. 2015).

Taken together, these findings suggest that rTPJ acts as a hub for high-level perspective taking by routing visual information to internal representations of the self, the body and its action and posture repertoire, via theta-band phase synchronisation (Figure 4). This allows humans to actively project their own sense of self into another's viewpoint, resulting in rapid and accurate perspective-taking responses (Kessler and Rutherford 2010; Surtees et al. 2013; Wang et al. 2016; Gooding-Williams et al. 2017). However, given the simplicity of the stimuli and required decisions (left or right) the social relevance of the current task and associated processing could be called into question. Therefore, we would like to point out that Kessler and Wang (2012) reported that social skills (social skills subscale of the AQ, Baron-Cohen et al., 2001) and gender significantly predicted speed and embodiment of responses on this task, suggesting that social abilities are linked to embodied perspective taking even in this repetitive and simplified experimental form. Furthermore, using exactly the same tasks, Kessler et al (2014,Proc R Soc B) showed that while the basic mechanisms for perspective-taking and -tracking are essentially the same for Western and East-Asian participants, there are subtle but significant culture-related differences in terms of self- vs. other-centred biases that have been interpreted as cultural manifestations of differing social norms (e.g. Markus and Kitayama, 1991; also Wu, Barr, Gann, & Keysar, 2013).Finally, Bögels et al (2015) reported very similar theta oscillatory coupling between right TPJ and

mPFC during a more complex task of social perspective taking, where participants needed to judge whether an interactor in a different room was presented with the same visual object or not, based on their previous communication. This is a genuinely social task in the sense of imagining another person's current visual experience with the aim to enable successful communication. During this high-level social task right TPJ was phase-coherent with vmPFC, thus confirming our claim that this coupling is part of the basic mechanism for simpler as well as for more sophisticated forms of social mental alignment.

Interestingly, the other side of the coin of the described embodied perspective-taking process tied to TPJ seems to be that aberrant activity in TPJ contributes to involuntary shifts in perspective, as experienced in so-called "out-of–body" experiences (OBE) (Blanke et al. 2005; Kessler and Braithwaite 2016). This emerging framework is consistent with a recent model arguing that the TPJ acts as a "nexus", hub, or convergence zone between different cognitive domains including social cognition, attention and executive function (Carter and Huettel 2013). Our results suggest that the TPJ plays an important role during complex social-cognitive processes like perspective-taking, by co-ordinating the activity between multiple brain regions and functional sub-networks into a coherent whole (Santiesteban et al. 2012; Carter and Huettel 2013; Bögels et al. 2015; Eddy 2016) (Fig. 4). We further propose that theta oscillations could be the crucial network code for this integration process (Bögels et al. 2015; Wang et al. 2016; Gooding-Williams et al. 2017).

Top-down Executive Processes during high-level perspective-taking

Along with the rTPJ, two additional regions showed significantly increased theta power with increasing angular disparity during perspective-taking (Fig. 2A): the lateral PFC, primarily overlapping with the right inferior frontal gyrus; and the right ACC. This theta-band activity

was found during a slightly later period than the rTPJ, from 0.2-0.5 post-stimulus onset, suggesting that the ACC and lateral PFC contribute later to the process of perspective-taking. Interestingly, we also found that these two regions displayed directed functional connectivity, as measured by Granger causality, to the rTPJ, mediated by low frequency brain rhythms (1-10Hz), indicative of top-down processing (Von Stein et al. 2000).

Activity within the ACC and lateral PFC is typically associated with cognitive control (Aron et al. 2014) and conflict monitoring (Botvinick et al. 2004). However recent work has shown the regions to be also implicated in a number of theory of mind studies (Vogeley et al. 2001; Hartwright et al. 2012, 2015; Samson et al. 2015). Activity within this context has been argued to reflect the detection (Amodio and Frith 2006; Lieberman 2007) (ACC) and resolution (Samson et al. 2005; Hartwright et al. 2012) (lateral PFC) of conflict between self and other perspectives (Hartwright et al. 2016a). We therefore propose (Fig. 4) that the connectivity from rACC and rPFC to rTPJ, during later stages of perspective-taking, reflects domain-general "top-down" executive control processes (Duncan and Owen 2000) required for suppressing the self-perspective, in favour of taking the other's perspective (Samson et al. 2005; Van der Meer et al. 2011; Hartwright et al. 2015), and/or for controlling the conflict between the physical self and the transformed self (the "other") (May 2004; Santiesteban et al. 2012; Wang et al. 2016), allowing both representations to co-exist in the brain, similar to the experience of an OBE, where the self is located in two places at once (Kessler and Braithwaite 2016). Our results differ slightly from those reported in (McCleery et al. 2011), but our interpretations are not fully at odds with McCleery et al's, who argue that the lateral PFC selects between self/other perspectives, both computed in the rTPJ, depending on task demands, thus, favouring our second interpretation (i.e., ACC and lateral PFC managing the conflict between self and other perspectives that may coexist in TPJ). At this stage it remains

unknown what information content exactly is computed in which part of the brain. Differing results could also be due to differences in the paradigms employed – unlike (McCleery et al. 2011), perspective-taking stimuli in this study required differing levels of embodied simulation, potentially requiring different levels of conflict management between self and other perspectives. In addition, this study focussed on earlier frontal theta-band oscillations (0-0.65s) compared with the later evoked frontal responses (0.6-0.8s) reported in (McCleery et al. 2011). It should also be noted that perspective-tracking could also involve similar cognitive control processes. However, the experimental contrast between different angular disparities (160° vs 60°) may have precluded our ability to detect this, as similar executive control processes would be equally engaged in both conditions.

More generally, whilst the involvement of executive-control processes in perspective-taking is based on substantial empirical research (Aron et al. 2014; Hartwright et al. 2016a), to avoid reverse-inference, future work could vary executive demands during perspective-taking (Bradford et al. 2015), in combination with brain stimulation (Wang et al. 2016) to establish the causal role of the lateral PFC and rACC. For example, one study has shown that theta-burst TMS to lateral PFC slowed reaction times during a false belief task requiring a dissociation between self and other perspectives, after modelling the structural morphology of lateral PFC and right TPJ (Hartwright et al. 2016b). In addition, the observation that our effects in ACC and PFC were primarily related to theta oscillations, further corroborates the notion of top-down control, since theta has previously been shown to reflect top-down cognitive control processes involved in conflict monitoring (Botvinick et al. 2004) and error-related responses (Trujillo and Allen 2007). Our complimentary finding that the ACC and lateral PFC exerted top-down influence on the TPJ via low frequency rhythms (1-10Hz,

peaking in theta) is clearly consistent with ACC and PFC theta as a mechanism for cognitive control.

Limitations

This article, building on our previous work (Bögels et al. 2015; Wang et al. 2016; Gooding-Williams et al. 2017), has focussed on the role of theta-band power and connectivity underlying perspective-taking. Whilst sensor-level analysis revealed only a single positive cluster of activity from 3-6Hz, corroborating our previous results, inspection of Figure 2A suggests that these effects might spread into delta and low alpha frequency ranges. This is also observed for right TPJ (power) and lateral PFC which peaks in delta (1-3Hz) rather than theta (3-6Hz) in power and Granger causality spectra (Fig. 2). This discrepancy may explain the lack of phase synchrony, probed at 5±2 Hz rather than 1-3Hz, between the right TPJ and lateral PFC reported using imaginary coherence. It is worth noting that the fine-grained definition of frequency ranges is confounded by spectral smoothing applied during the frequency decomposition process. Future work should therefore attempt to clarify whether there might be additional independent or multiplexed oscillatory networks (e.g. Seymour et al. 2017) at different frequency ranges, including those between delta/theta and gamma (>30Hz) bands (Cao et al. 2018). Nevertheless, this article suggests that theta (3-6Hz) appears to be the most dominant oscillatory frequency band (if not the only band), underlying embodied perspective-taking.

Conclusion

This study examined the cortical networks involved in high-level mental alignment (perspective taking), co-ordinated by theta-band oscillations. Low-frequency phase coupling in the theta-band, has previously been shown to contribute to the co-ordination of long-range

neuronal interactions (von Stein and Sarnthein 2000; Mizuhara et al. 2004), through which distributed neural assemblies become integrated into a coherent network (Varela et al. 2001). Our finding that theta-band phase-coupling synchronises the right temporo-parietal junction (rTPJ) to brain regions involved in theory of mind and regions coding for body schema supports this view, and suggests that perspective taking, and potentially other social cognitive processes, involve the co-ordination of spatially and functionally disperse brain regions via theta-band phase synchrony (von Stein and Sarnthein 2000), further supported by low-frequency top-down influences from executive control areas (Bögels et al. 2015).

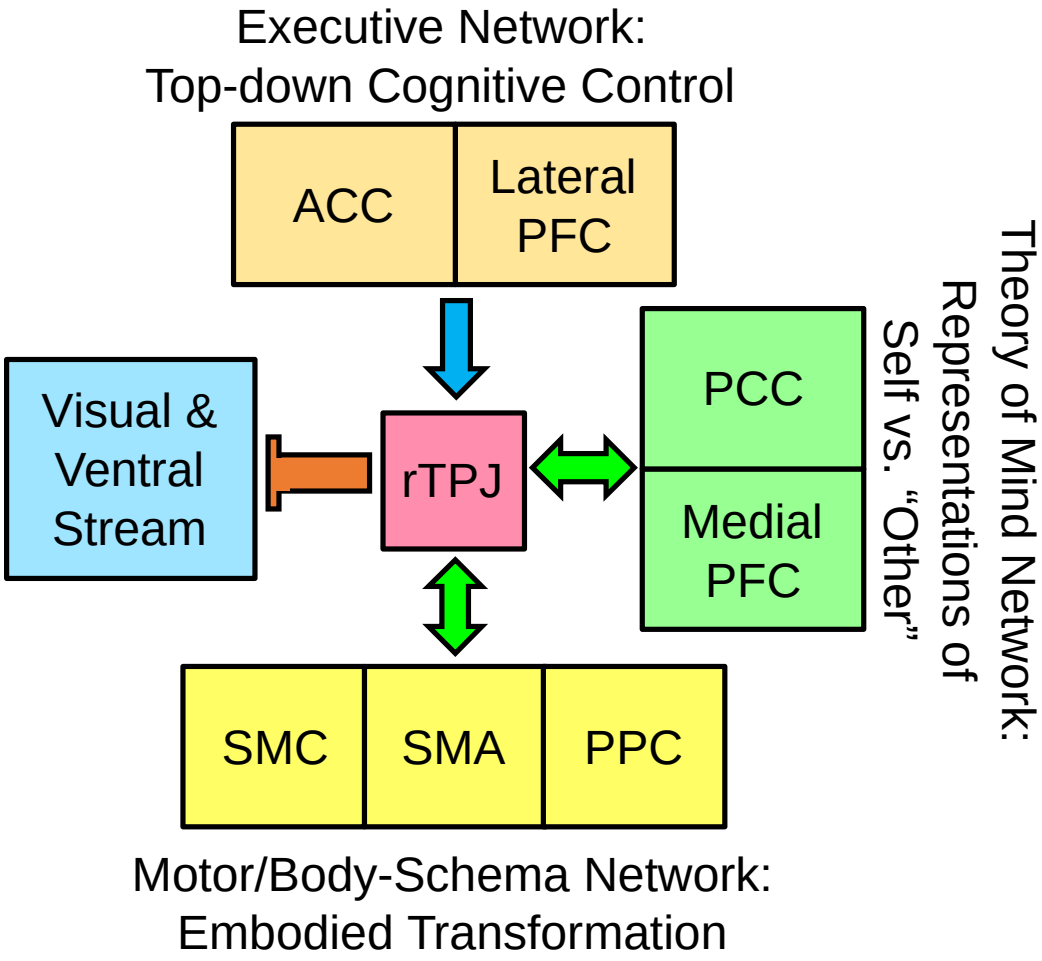


Figure 4: Proposed network underlying high-level perspective-taking (Kessler and Rutherford 2010; Surtees et al. 2013), linked by power and phase in the theta-band (3-7Hz).

During initiation of embodied perspective-taking behaviour, early rTPJ activity co-ordinates connectivity decreases with visual regions, whilst increasing connectivity with regions involved in Theory of Mind, and Motor/Body-Schema. Increases in low frequency (primarily theta) power within the lateral PFC and ACC reflect domain-general cognitive control processes for detecting and managing top-down the conflict between self and other perspectives.

Acknowledgements

We wish to thank Gerard Gooding-Williams for MRI acquisition and the Wellcome and Dr. Hadwen Trusts for supporting MEG scanning costs. RS was supported by a Cotutelle Ph.D. studentship from Aston University and Macquarie University.

References:

Amodio DM, Frith CD. 2006. Meeting of minds: the medial frontal cortex and social cognition. Nat Rev Neurosci. 7:268.

Aron AR, Robbins TW, Poldrack RA. 2014. Inhibition and the right inferior frontal cortex: one decade on. Trends Cogn Sci. 18:177–185.

Arzy S, Thut G, Mohr C, Michel CM, Blanke O. 2006. Neural Basis of Embodiment: Distinct Contributions of Temporoparietal Junction and Extrastriate Body Area. J Neurosci. 26:8074–8081.

Baron-Cohen S, Wheelwright, S , Skinner R, Martin J, & Clubley, E. 2001. The autism-spectrum quotient (AQ): Evidence from asperger syndrome/high-functioning autism, malesand females, scientists and mathematicians. Journal of autism and developmental disorders, 31:1, 5-17.

Bastos AM, Schoffelen J-M. 2016. A Tutorial Review of Functional Connectivity Analysis Methods and Their Interpretational Pitfalls. Front Syst Neurosci. 175.

Blanke O, Mohr C, Michel CM, Pascual-Leone A, Brugger P, Seeck M, Landis T, Thut G. 2005. Linking out-of-body experience and self processing to mental own-body imagery at the temporoparietal junction. J Neurosci. 25:550–557.

Bögels S, Barr DJ, Garrod S, Kessler K. 2015. Conversational interaction in the scanner: mentalizing during language processing as revealed by MEG. Cereb Cortex. 25:3219–3234.

Botvinick MM, Cohen JD, Carter CS. 2004. Conflict monitoring and anterior cingulate cortex: an update. Trends Cogn Sci. 8:539–546.

Bradford EEF, Jentzsch I, Gomez J-C. 2015. From self to social cognition: Theory of Mind mechanisms and their relation to Executive Functioning. Cognition. 138:21–34.

Bräuer J, Call J, Tomasello M. 2007. Chimpanzees really know what others can see in a competitive situation. Anim Cogn. 10:439–448.

Brookes MJ, Hale JR, Zumer JM, Stevenson CM, Francis ST, Barnes GR, Owen JP, Morris PG, Nagarajan SS. 2011. Measuring functional connectivity using MEG: methodology and comparison with fcMRI. Neuroimage. 56:1082–1104.

Bugnyar T, Stöwe M, Heinrich B. 2004. Ravens, Corvus corax, follow gaze direction of humans around obstacles. Proc R Soc Lond B Biol Sci. 271:1331–1336.

Bzdok D, Langner R, Schilbach L, Jakobs O, Roski C, Caspers S, Laird AR, Fox PT, Zilles K, Eickhoff SB. 2013. Characterization of the temporo-parietal junction by combining data-driven parcellation, complementary connectivity analyses, and functional decoding. NeuroImage. 81:381–392.

Call J, Tomasello M. 1999. A nonverbal false belief task: The performance of children and great apes. Child Dev. 70:381–395.

Cao W, Lin S, Xia Q, Du Y, Yang Q, Zhang M, Lu Y, Xu J, Duan S, Xia J, Feng G, Xu J, Luo J. 2018. Gamma Oscillation Dysfunction in mPFC Leads to Social Deficits in Neuroligin 3 R451C Knockin Mice. Neuron. 97:1253-1260.e7.

Carrington SJ, Bailey AJ. 2009. Are there theory of mind regions in the brain? A review of the neuroimaging literature. Hum Brain Mapp. 30:2313–2335.

Carter RM, Huettel SA. 2013. A nexus model of the temporal–parietal junction. Trends Cogn Sci. 17:328–336.

Cazzato V, Mian E, Serino A, Mele S, Urgesi C. 2015. Distinct contributions of extrastriate body area and temporoparietal junction in perceiving one's own and others' body. Cogn Affect Behav Neurosci. 15:211–228.

Coslett H, Buxbaum LJ, Schwoebel J. 2008. Accurate reaching after active but not passive movements of the hand: Evidence for forward modeling. Behav Neurol. 19:117–125.

Dhamala M, Rangarajan G, Ding M. 2008. Analyzing information flow in brain networks with nonparametric Granger causality. Neuroimage. 41:354–362.

Ding Mingzhou, Chen Yonghong, Bressler Steven L. 2006. Granger Causality: Basic Theory and Application to Neuroscience. Handb Time Ser Anal, Wiley Online Books.

Duncan J, Owen AM. 2000. Common regions of the human frontal lobe recruited by diverse cognitive demands. Trends Neurosci. 23:475–483.

Eddy CM. 2016. The junction between self and other? Temporo-parietal dysfunction in neuropsychiatry. Neuropsychologia. 89:465–477.

Engel AK, Fries P, Singer W. 2001. Dynamic predictions: Oscillations and synchrony in top–down processing. Nat Rev Neurosci. 2:704–716.

Flavell JH, Everett BA, Croft K, Flavell ER. 1981. Young children's knowledge about visual perception: Further evidence for the Level 1–Level 2 distinction. Dev Psychol. 17:99.

Frith CD, Frith U. 2007. Social cognition in humans. Curr Biol. 17:R724–R732.

Garcia D. 2010. Robust smoothing of gridded data in one and higher dimensions with missing values. Comput Stat Data Anal. 54:1167–1178.

Gooding-Williams G, Wang H, Kessler K. 2017. THETA-Rhythm Makes the World Go Round: Dissociative Effects of TMS Theta Versus Alpha Entrainment of Right pTPJ on Embodied Perspective Transformations. Brain Topogr. 1–4.

Gross s J, Kujala J, Hämäläinen M, Timmermann L, Schnitzler A, Salmelin R. 2001. Dynamic imaging of coherent sources: studying neural interactions in the human brain. Proc Natl Acad Sci. 98:694–699.

Gzesh SM, Surber CF. 1985. Visual perspective-taking skills in children. Child Dev. 1204–1213.

Hartwright CE, Apperly IA, Hansen PC. 2012. Multiple roles for executive control in belief–desire reasoning: Distinct neural networks are recruited for self perspective inhibition and complexity of reasoning. NeuroImage. 61:921–930.

Hartwright CE, Apperly IA, Hansen PC. 2015. The special case of self-perspective inhibition in mental, but not non-mental, representation. Neuropsychologia. 67:183–192.

Hartwright CE, Hansen PC, Apperly IA. 2016a. Current knowledge on the role of the Inferior Frontal Gyrus in Theory of Mind – A commentary on Schurz and Tholen (2016). Cortex. 85:133–136.

Hartwright Charlotte E., Hardwick Robert M., Apperly Ian A., Hansen Peter C. 2016b. Resting state morphology predicts the effect of theta burst stimulation in false belief reasoning. Hum Brain Mapp. 37:3502–3514.

Igelström KM, Graziano MSA. 2017. The inferior parietal lobule and temporoparietal junction: A network perspective. Neuropsychologia.

Jenkinson M, Smith S. 2001. A global optimisation method for robust affine registration of brain images. Med Image Anal. 5:143–156.

Kessler K, Braithwaite JJ. 2016. Deliberate and spontaneous sensations of disembodiment: capacity or flaw? Cognit Neuropsychiatry. 21:412–428.

Kessler K, Cao L, O'Shea K J, Wang H. 2014. A cross-culture, cross-gender comparison of perspective taking mechanisms. Proceedings of the Royal Society of London B: Biological Sciences, 281:1785, 20140388.

Kessler K, Rutherford H. 2010. The Two Forms of Visuo-Spatial Perspective Taking are Differently Embodied and Subserve Different Spatial Prepositions. Front Psychol. 1:213.

Kessler K, Thomson LA. 2010. The embodied nature of spatial perspective taking: embodied transformation versus sensorimotor interference. Cognition. 114:72–88.

Kessler, K, Wang, H. 2012. Spatial perspective taking is an embodied process, but not for everyone in the same way: differences predicted by sex and social skills score. Spatial Cog & Comp, 12:2-3, 133-158.

Lieberman MD. 2007. Social cognitive neuroscience: a review of core processes. Annu Rev Psychol. 58:259–289.

Lombardo MV, Chakrabarti B, Bullmore ET, Wheelwright SJ, Sadek SA, Suckling J, Baron-Cohen S, Consortium MA, others. 2010. Shared neural circuits for mentalizing about the self and others. J Cogn Neurosci. 22:1623–1635.

Maris E, Oostenveld R. 2007. Nonparametric statistical testing of EEG- and MEG-data. J Neurosci Methods. 164:177–190.

Markus HR, Kitayama S. 1991. Culture and the self: Implications for cognition, emotion, and motivation. Psychological review, 98:2, 224.

Mars RB, Sallet J, Schüffelgen U, Jbabdi S, Toni I, Rushworth MF. 2012. Connectivity-based subdivisions of the human right “temporoparietal junction area”: evidence for

different areas participating in different cortical networks. Cereb Cortex. 22:1894–1903.

May M. 2004. Imaginal perspective switches in remembered environments: Transformation versus interference accounts. Cognit Psychol. 48:163–206.

McCleery JP, Surtees ADR, Graham KA, Richards JE, Apperly IA. 2011. The Neural and Cognitive Time Course of Theory of Mind. J Neurosci. 31:12849–12854.

Medina J, Jax SA, Coslett HB. 2009. Two-component models of reaching: Evidence from deafferentation in a Fitts' law task. Neurosci Lett. 451:222–226.

Mizuhara H, Wang L-Q, Kobayashi K, Yamaguchi Y. 2004. A long-range cortical network emerging with theta oscillation in a mental task. Neuroreport. 15:1233–1238.

Moll H, Tomasello M. 2006. Level 1 perspective-taking at 24 months of age. Br J Dev Psychol. 24:603–613.

Nolte G. 2003. The magnetic lead field theorem in the quasi-static approximation and its use for magnetoencephalography forward calculation in realistic volume conductors. Phys Med Biol. 48:3637–3652.

Nolte G, Bai O, Wheaton L, Mari Z, Vorbach S, Hallett M. 2004. Identifying true brain interaction from EEG data using the imaginary part of coherency. Clin Neurophysiol Off J Int Fed Clin Neurophysiol. 115:2292–2307.

Oostenveld R, Fries P, Maris E, Schoffelen J-M. 2010. FieldTrip: open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. Comput Intell Neurosci. 2011.

Povinelli DJ, Bering JM, Giambrone S. 2000. Toward a science of other minds: Escaping the argument by analogy. Cogn Sci. 24:509–541.

Samson D, Apperly IA, Kathirgamanathan U, Humphreys GW. 2005. Seeing it my way: a case of a selective deficit in inhibiting self-perspective. Brain. 128:1102–1111.

Samson D, Houthuys S, Humphreys GW. 2015. Self-perspective inhibition deficits cannot be explained by general executive control difficulties. Cortex. 70:189–201.

Santiesteban I, Banissy MJ, Catmur C, Bird G. 2012. Enhancing social ability by stimulating right temporoparietal junction. Curr Biol. 22:2274–2277.

Schurz M, Aichhorn M, Martin A, Perner J. 2013. Common brain areas engaged in false belief reasoning and visual perspective taking: a meta-analysis of functional brain imaging studies. Front Hum Neurosci. 7.

Schurz M, Kronbichler M, Weissengruber S, Surtees A, Samson D, Perner J. 2015. Clarifying the role of theory of mind areas during visual perspective taking: Issues of spontaneity and domain-specificity. NeuroImage. 117:386–396.

Seymour RA. 2017. Neurofractal/perspective_taking_oscillatory_networks: Work in Progress Release of Perspective Taking Data.

Seymour RA, Rippon G, Kessler K. 2017. The Detection of Phase Amplitude Coupling during Sensory Processing. Front Neurosci. 11:487.

Sowden S, Catmur C. 2015. The role of the right temporoparietal junction in the control of imitation. Cereb Cortex. 25:1107–1113.

Surtees A, Apperly I, Samson D. 2013. The use of embodied self-rotation for visual and spatial perspective-taking. Front Hum Neurosci. 7.

Tomasello M, Carpenter M, Call J, Behne T, Moll H. 2005. Understanding and sharing intentions: the origins of cultural cognition. Behav Brain Sci. 28:675–691; discussion 691-735.

Trujillo LT, Allen JJ. 2007. Theta EEG dynamics of the error-related negativity. Clin Neurophysiol. 118:645–668.

Van der Meer L, Groenewold NA, Nolen WA, Pijnenborg M, Aleman A. 2011. Inhibit yourself and understand the other: neural basis of distinct processes underlying Theory of Mind. Neuroimage. 56:2364–2374.

Van Essen DC, Ugurbil K, Auerbach E, Barch D, Behrens TEJ, Bucholz R, Chang A, Chen L, Corbetta M, Curtiss SW, others. 2012. The Human Connectome Project: a data acquisition perspective. Neuroimage. 62:2222–2231.

Van Overwalle F. 2009. Social cognition and the brain: A meta-analysis. Hum Brain Mapp. 30:829–858.

Van Overwalle F. 2011. A dissociation between social mentalizing and general reasoning. Neuroimage. 54:1589–1599.

Van Overwalle F, Baetens K. 2009. Understanding others' actions and goals by mirror and mentalizing systems: a meta-analysis. Neuroimage. 48:564–584.

Varela F, Lachaux J-P, Rodriguez E, Martinerie J. 2001. The brainweb: phase synchronization and large-scale integration. Nat Rev Neurosci. 2:229–239.

Vincent JL, Kahn I, Snyder AZ, Raichle ME, Buckner RL. 2008. Evidence for a frontoparietal control system revealed by intrinsic functional connectivity. J Neurophysiol. 100:3328–3342.

Vogeley K, Bussfeld P, Newen A, Herrmann S, Happé F, Falkai P, Maier W, Shah NJ, Fink GR, Zilles K. 2001. Mind reading: neural mechanisms of theory of mind and self-perspective. Neuroimage. 14:170–181.

Von Stein A, Chiang C, König P. 2000. Top-down processing mediated by interareal synchronization. Proc Natl Acad Sci. 97:14748–14753.

von Stein A, Sarnthein J. 2000. Different frequencies for different scales of cortical integration: from local gamma to long range alpha/theta synchronization. Int J Psychophysiol. 38:301–313.

Wang H, Callaghan E, Gooding-Williams G, McAllister C, Kessler K. 2016. Rhythm makes the world go round: An MEG-TMS study on the role of right TPJ theta oscillations in embodied perspective taking. Cortex J Devoted Study Nerv Syst Behav. 75:68–81.

Womelsdorf T, Schoffelen J-M, Oostenveld R, Singer W, Desimone R, Engel AK, Fries P. 2007. Modulation of neuronal interactions through neuronal synchronization. Science. 316:1609–1612.

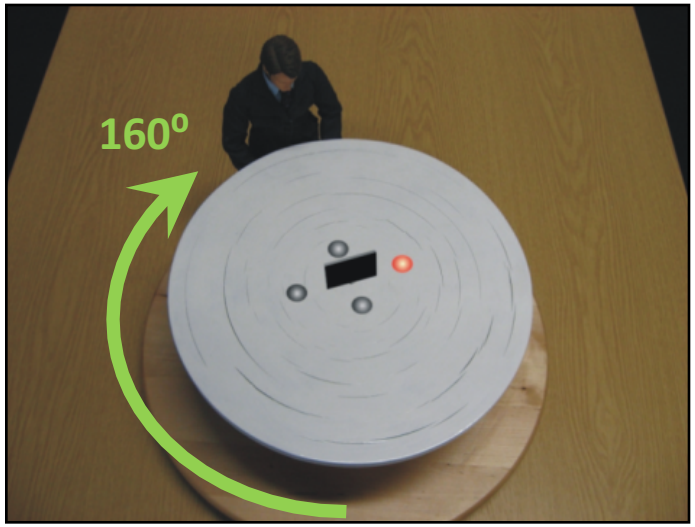
Wu S, Barr DJ, Gann TM, Keysar B. 2013. How culture influences perspective taking: differences in correction, not integration. Frontiers in human neuroscience, 7, 822.

Wu Q, Chang C-F, Xi S, Huang I-W, Liu Z, Juan C-H, Wu Y, Fan J. 2015. A critical role of temporoparietal junction in the integration of top-down and bottom-up attentional control. Hum Brain Mapp. 36:4317–4333.

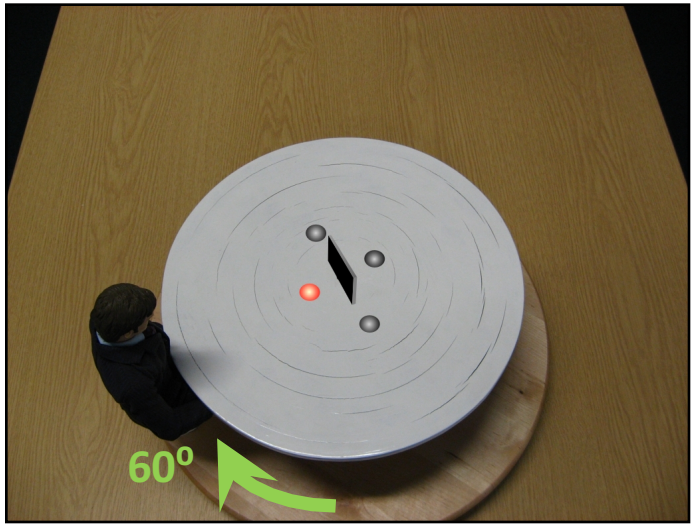
Zacks JM, Michelon P. 2005. Transformations of visuospatial images. Behav Cogn Neurosci Rev. 4:96–118.

"left or right?"

Target = 160º Hard

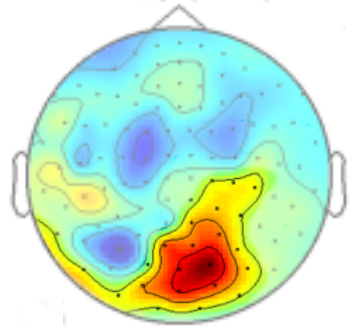


Target = 60º Easy

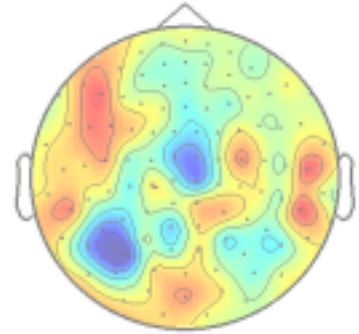


"visible or occluded?"

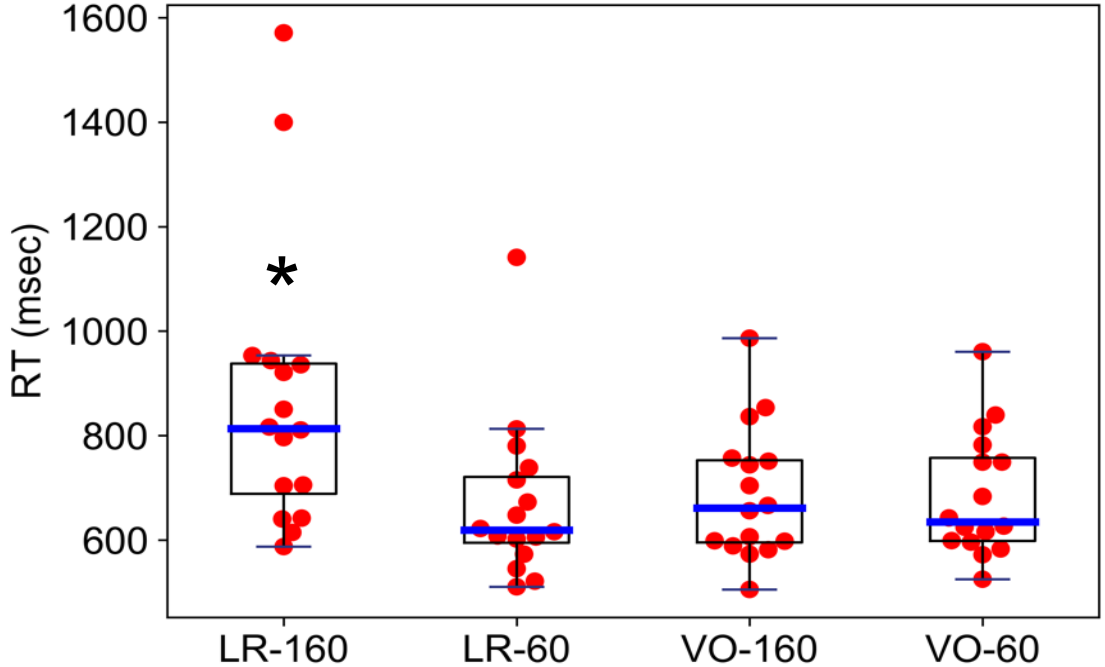
Theta 3-6Hz; 0-650ms post-stimulus onset



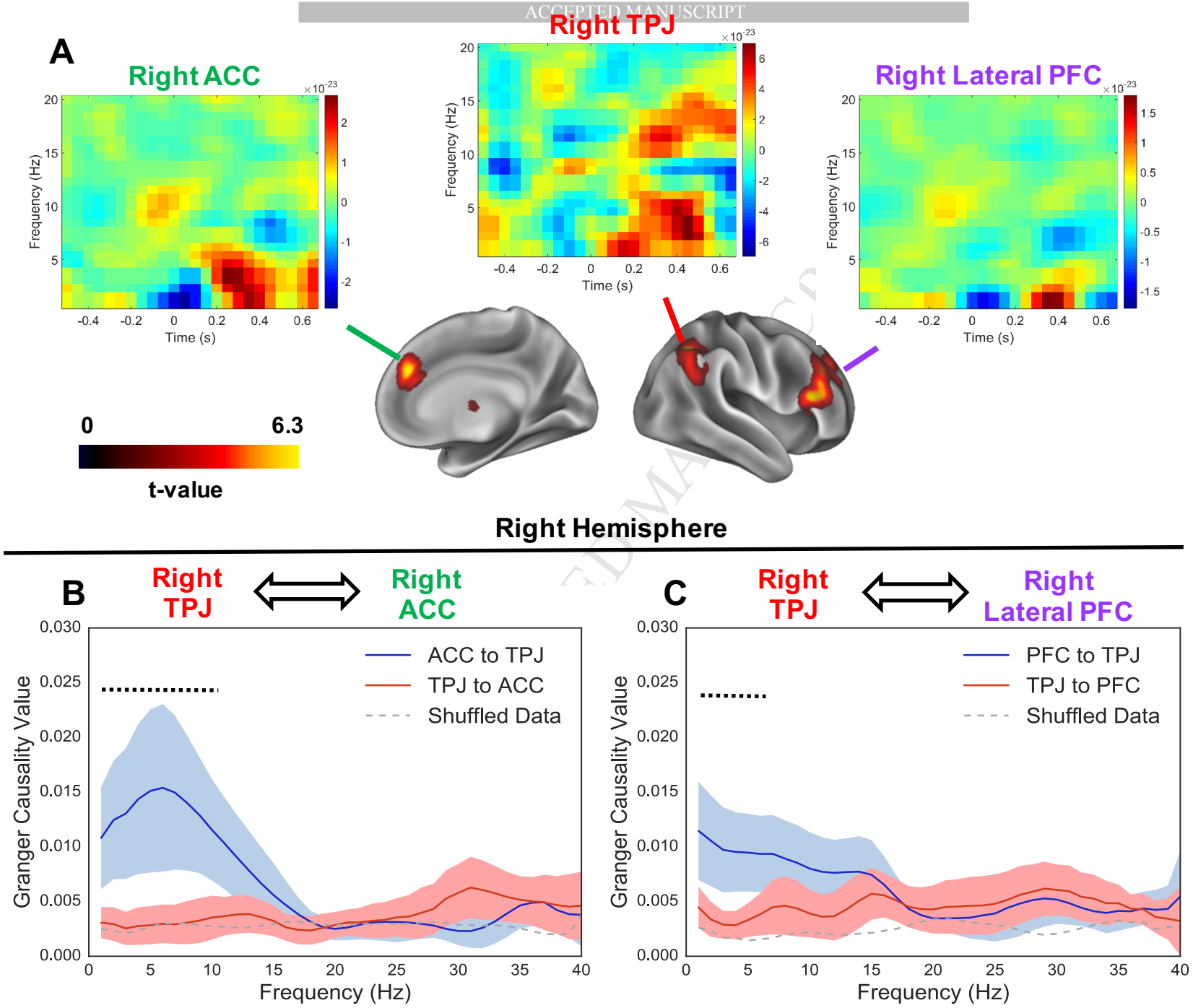
LR-160 > LR-60

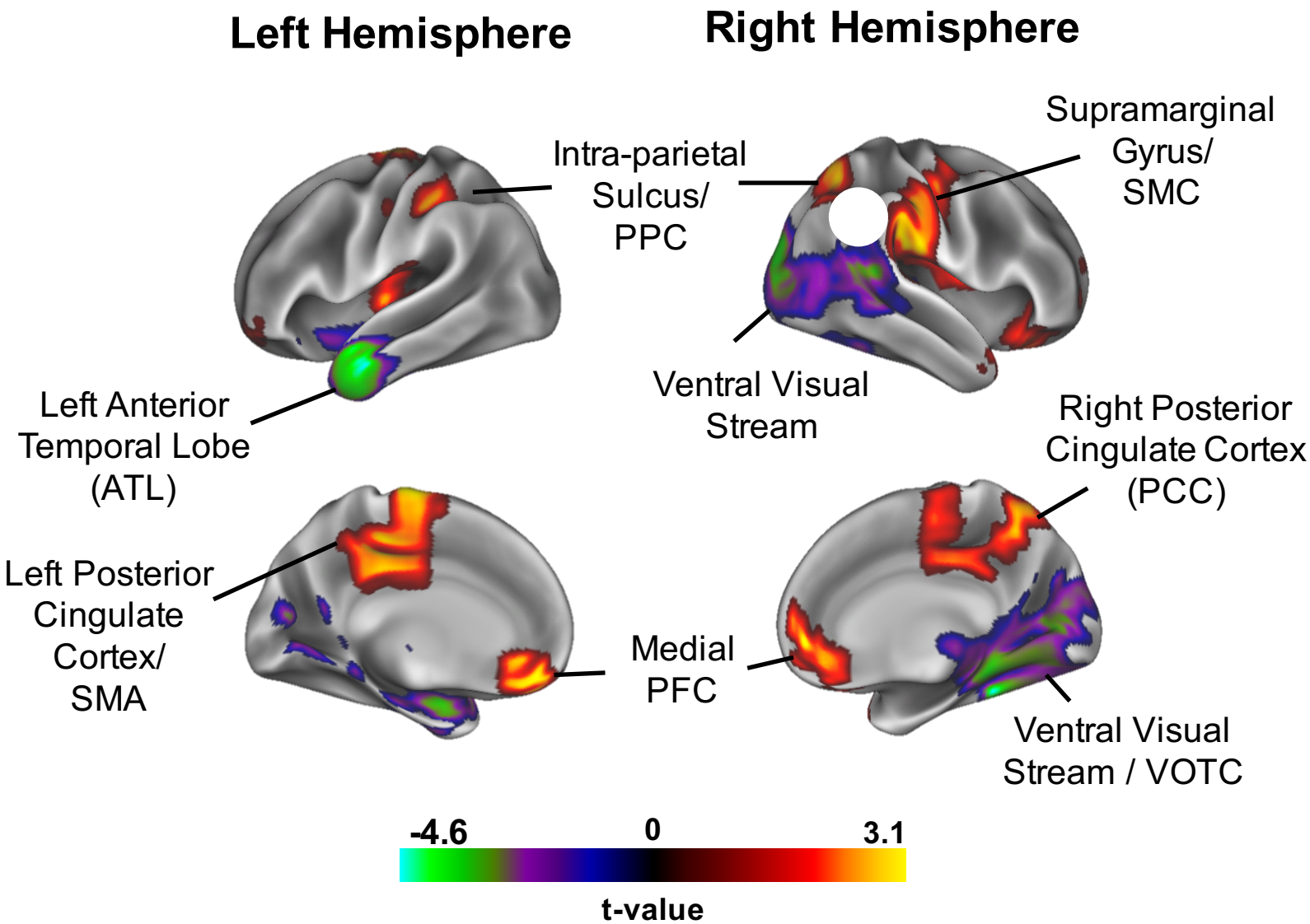


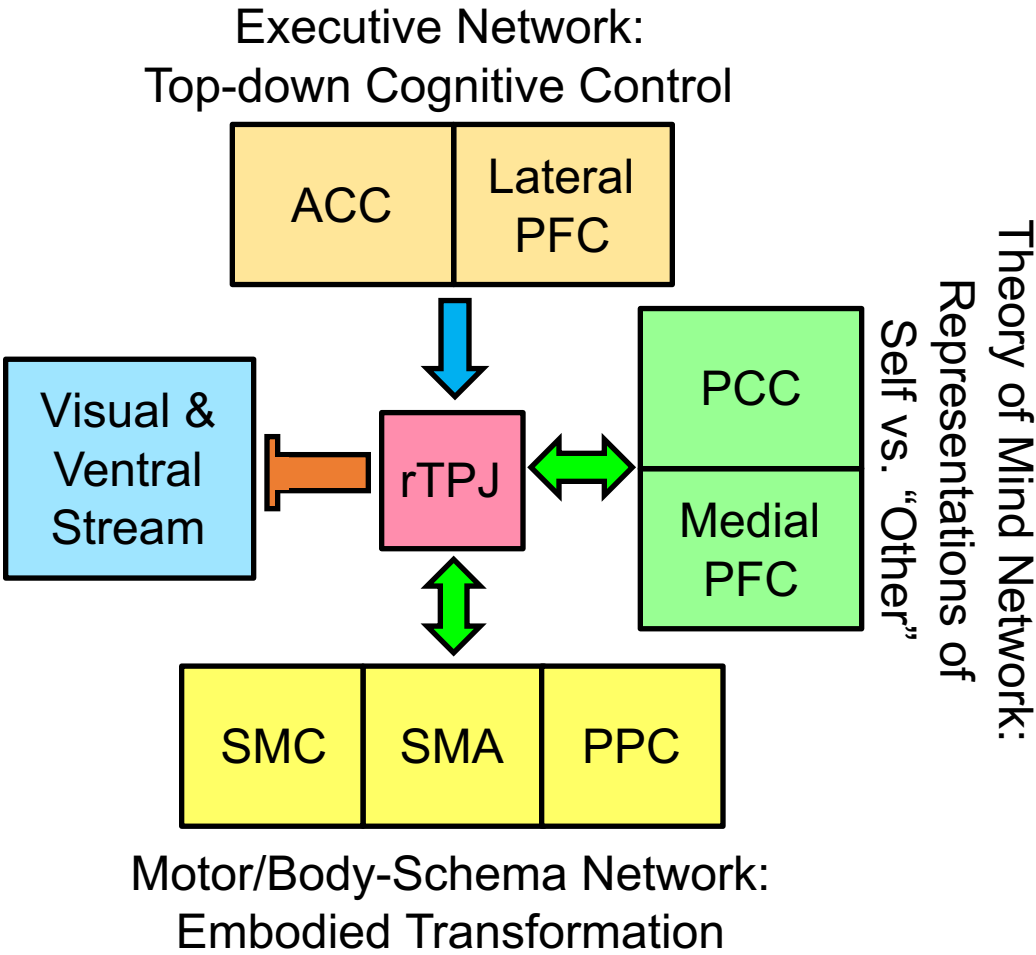
VO-160 > VO-60



"left or right?" *"visible or occluded?"*




Left Hemisphere
Right Hemisphere
Intra-parietal Sulcus/ PPC
Supramarginal Gyrus/ SMC
Ventral Visual Stream
Left Anterior Temporal Lobe (ATL)
Right Posterior Cingulate Cortex (PCC)
Left Posterior Cingulate Cortex/ SMA
Medial PFC
Ventral Visual Stream / VOTC
-4.6
0
3.1
t-value


Executive Network:
Top-down Cognitive Control
ACC
Lateral PFC
Visual & Ventral Stream
rTPJ
PCC
Medial PFC
Theory of Mind Network:
Representations of Self vs. "Other"
SMC
SMA
PPC
Motor/Body-Schema Network:
Embodied Transformation