



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

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### 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 (3–7 Hz) 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 prefrontal 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.

### 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;

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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 (6 Hz) accelerated perspective-taking, while alpha (10 Hz) 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 450 ms, 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 prefrontal 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)mpPFC 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 IPFC 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 presented black screen (occluder); 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

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