The Coherent Default Mode Network is not involved in Episodic Recall or Social Cognition

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Short title: Testing the DMNs Function

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Abstract

Resting-state network research is extremely influential, yet the functions of many networks remain unknown. Hypotheses implicating the default mode network (DMN) in episodic memory and social cognition are highly popular. Univariate analyses and meta-analyses of these functions show activation in similar regions to the DMN. However, this does not necessitate the involvement of the coherent network in these functions. Here we formally test the role of the coherent DMN in episodic and social processing. As well as an episodic retrieval task, two independent datasets were employed to assess the breadth of social cognition; a person knowledge judgement and a theory of mind task. Independent component analysis separated each task dataset into coherent networks. For each, the core DMN was identified through comparison to an *a priori* template and its relation to the task model was assessed. The DMN did not show greater activity in episodic or social tasks than in high-level baseline conditions. Thus, no evidence was found for the involvement of the coherent DMN in explicit episodic or social processing tasks. The networks responsible for these processes are described and the univariate findings considered in light of these findings. Implications for the functional significance of the DMN are considered.

Introduction

Most higher cognitive functions are not localised to a single brain region but rather reflect the joint action of a distributed network of regions (Mesulam 1990; Catani et al. 2012; Humphreys et al. 2014). The role of a brain area is determined by its current 'neural context'; its interactions with other connected regions (McIntosh 1999; Chen et al. 2017). This necessitates the use of network-level approaches to understand function. Coherent networks of co-activated brain regions can be extracted from the time-course of resting-state fMRI data (i.e., data acquired without a formal task) using Independent Component Analysis (ICA; Beckmann et al. 2005; Calhoun et al. 2008; Smith et al. 2009; Geranmayeh et al. 2012; Geranmayeh et al. 2014). These 'resting-state networks' (RSNs) reflect connectivity identifiable in multiple task states (earning them the alternative name 'Intrinsic Connectivity Networks'; Smith et al. 2009; Laird et al. 2011), yet a single run of resting-state data is far easier to acquire. The ease of collection of resting-state fMRI potentially licenses the use of RSNs in both basic and clinical neurosciences and has led to a recent explosion of interest across different disciplines (Rosazza et al. 2011; de la Iglesia-Vaya et al. 2013). In particular, there is great interest in one specific RSN, the default mode network (DMN). The DMN was initially defined as the areas that were more active during rest than in most tasks (Shulman et al. 1997; Raichle et al. 2001), yet has been shown to reflect a coherent network that can be identified during rest and task states (Greicius et al. 2003; Buckner et al. 2008). Areas associated with the DMN include medial prefrontal cortex, posterior cingulate cortices, precuneus, angular gyrus and lateral and medial temporal cortices, although the central focus is the medial surface (Raichle et al. 2001; Buckner et al. 2008; Utevsky et al. 2014).

Despite its popularity RSN research is currently missing a vital aspect, impairing the ability of researchers to interpret related findings. RSNs are inherently detached from function due to the lack of functional information during the scan. If the associations between RSNs and function remain unknown, it may limit the impact of the large amount of RSN research on cognitive

neuroscience (which, by definition, aims to explain the relationship between cognition and the brain). Despite the lack of functional information in resting-state data, a number of functions of the DMN have been postulated. Finding greater activity in DMN regions in rest compared to various tasks led to the theory that the DMN is simply performing some process that occurs frequently during free thought, yet could occur in an active task if the appropriate domain was tested (Buckner et al. 2008; Callard et al. 2012). Within this framework three popular candidate processes have been postulated; episodic memory, social cognition and semantic cognition (Binder et al. 1999; Buckner et al. 2008; Binder et al. 2009; Mars et al. 2012). Evidence in favour of a critical role of the DMN in these processes was predominantly gained from visual comparison of the spatial extent of the DMN and univariate (including meta-analytic) results of task activation related to each process (Binder et al. 1999; Buckner et al. 2008; Binder et al. 2009; Kim 2010; Mars et al. 2012).

Despite the prevalence of these hypotheses, the relation of the coherent DMN to episodic and social cognition processes has yet to be directly probed. Visual comparison of the network extent and the results of a task-based subtraction analysis does not constitute a formal investigation of the networks cognition (Jackson et al. 2019). One critical issue is how to judge quantitatively rather than qualitatively whether spatial maps of a network and a univariate analysis result are sufficiently similar to reflect the same network. A second key issue is that there are multiple reasons why differences in task activation may occur in regions similar to those in a network without involvement of the coherent network in that domain. First, difficulty differences can result in the identification of areas responsible for task-general processing or that show task general deactivation, typically thought to involve similar areas to known resting-state networks (Vincent et al. 2008; Duncan 2010; Gilbert et al. 2012; Humphreys et al. 2014; Assem et al. 2020; Humphreys et al. submitted). Indeed if a task-related process is performed quicker within a trial in one condition, the extra remaining time means a greater amount of rest or off-task processing

will occur. This means that RSNs incidental to the task may show greater activity in this condition. Secondly, brain regions demonstrate dynamic connectivity and many are involved in multiple networks (Breakspear 2004; Hutchison et al. 2013). Thus, the involvement of one or more areas in a task does not necessitate the importance of a specific associated network. A region may be involved in a given function only when associated with one particular set of connections, which may or may not be the network of interest. Alternatively, an activation difference within one region may be due to the sum activity of two networks that overlap in that area. Therefore, only by testing the function of a coherent network (and not merely the average activity of each constituent region) can the involvement of the network *per se* be confirmed (Smith et al. 2009; Laird et al. 2011; Leech et al. 2011; Geranmayeh et al. 2012; Geranmayeh et al. 2014; Jackson et al. 2019).

Methods that do not detect a coherent network (including task-based deactivation and seed-based connectivity analyses) could also conflate the function of multiple, divisible RSNs. Evidence that task-negative regions may not reflect a single coherent network is provided by their task-dependent deactivation from rest (Humphreys et al. 2015), the differential task activation of constituent regions (Leech et al. 2011; Sestieri et al. 2011; Axelrod et al. 2017), and the division of these areas into different networks (Andrews-Hanna et al. 2010). For instance, not all of the regions that deactivate for most tasks deactivate in a semantic task, suggesting the core DMN is dissociable from the semantic network (Humphreys et al. 2015). Using ICA to identify coherent networks allowed separation of the semantic network and the core DMN, despite involvement of nearby or overlapping regions (Jackson et al. 2019). These dissociable networks may be conflated, in part, due to a moderate correlation in their time-courses caused by their mutual deactivation to many (but not all) tasks (Humphreys et al. 2015). Despite these spatial and temporal similarities, these coherent networks have distinct functional roles. Whilst the full set of regions that deactivate during many tasks (i.e., the 'default mode network' as

originally defined) does include both semantic and non-semantic regions, it is not meaningful to refer to these regions as one network and ascribe a function if they are neither strongly functionally connected nor fulfilling the same function. As resting-state assessments are detached from function, a coherent RSN-of-interest can be identified in the task state, allowing a formal test of its proposed function. This approach demonstrated that the coherent DMN was not involved in performance of an explicit semantic task, unlike the semantic network (Jackson et al. 2019). Thus, despite overlap between the DMN and the results of a meta-analysis of semantics (Binder et al. 2009; Binder et al. 2011), no evidence was identified for a role of the coherent DMN in semantic cognition. This may be, in part, due to difficulty differences in the contrasts used which themselves can generate false-positive functional interpretations of the DMN (Humphreys et al. 2015; Jackson et al. 2019; Jackson 2021).

In this study, we used the same approach to evaluate the hypotheses that the DMN is a network either for episodic or social processing, which have yet to be formally tested despite their prevalence. As social cognition may be multi-factorial (Van Overwalle 2009; Mars et al. 2012; Rice et al. 2018), two tasks evaluating diverse aspects of social cognition were employed; one testing the semantic processing of person knowledge and one engaging theory of mind processes.

Methods

Three previously-reported fMRI datasets including episodic and social tasks were analysed. These included one *Episodic Task,* one *Social - Person Knowledge Task* and one *Social - Theory of Mind Task*. The *Episodic* and the *Social - Person Knowledge* datasets employed dual echo EPI fMRI acquisition, improving signal in the problematic inferior frontal and temporal regions (including key medial prefrontal cortex areas) without loss of signal elsewhere (Poser et al. 2006; Halai et al. 2014). The *Social - Theory of Mind Task* was downloaded from the Human Connectome Project

(HCP; Barch et al. 2013; Van Essen et al. 2013). This does not have the benefit of dual echo EPI fMRI, but has a large number of participants, a high spatial resolution and processing steps designed to correct for signal distortion (Glasser et al. 2013; Van Essen et al. 2013).

The multi-step procedure outlined in Jackson et al., (2019) was followed. Analyses were performed separately for each task dataset. First, ICA was performed to determine the coherent networks present within the data. Secondly, the resting-state network-of-interest was identified through quantitative comparison of each resulting component to a template. This avoids the researcher bias present in visual comparison and helps determine whether one or more task components relates to the network-of-interest, i.e., whether the network has split and formed multiple components. In the final step, the functional role of the network-of-interest is tested by comparison to the task model. This provides a test of the function of the network *per se* and not merely the constituent regions, as for instance, ROI analyses would. For each task, a single contrast is used to determine whether the network-of-interest is involved in the condition of interest. These critical contrasts compare the task condition of interest to an active baseline as comparison to rest may be affected by the propensity of the process to occur during rest (Frackowiak 1991; Visser et al. 2010; Jackson et al. 2019). However, all plots are shown against rest for ease of interpretability across tasks.

Participants

In the *Episodic Task* data, 22 participants completed the study (18 females; mean age 24.55, SD 4.74). All were included in the present analyses. In the *Social - Person Knowledge Task*, data were acquired for 20 participants (16 female; mean age = 26.6 years, range = 20-42). One participant was excluded due to excessive motion (see Preprocessing Methods). The participant groups were independent with no participants involved in both studies. All had normal or corrected-to-

normal vision and hearing, and no history of psychiatric or neurological disorder. Both studies were approved by the local ethics board and all participants provided written informed consent.

The *Social - Theory of Mind Task* data was a subset of 80 participants of the Human Connectome Project 1200 Subject release (Van Essen et al. 2013). This number far exceeds the number of participants typically used in an fMRI study. Inclusion criteria for the HCP consisted of an age between 22 and 35 years and no significant history of psychiatric disorder, substance abuse, neurological, or cardiovascular disease. The first 40 male and 40 female participants with no data collection or analysis quality control issues were included in this study. All had an acquisition site of Washington University.

Imaging protocol

The *Episodic* and *Social - Person Knowledge* studies used the same scanner and a very similar acquisition protocol. Participants were scanned using a Phillips Achieva 3.0T system with a 32 channel SENSE coil with a sense factor of 2.5 whilst wearing noise cancelling Mk II+ headphones (MR Confon, Magdeburg, Germany). Structural references were obtained with an in-plane resolution of .938 and slice thickness of 1.173mm. Both studies utilised a dual gradient echo EPI technique to reduce signal dropout in inferior temporal and frontal cortex whilst maintaining contrast sensitivity throughout the brain (Poser et al. 2006; Poser et al. 2007, 2009; Halai et al. 2014). This involved parallel acquisition at a short (12ms) and a long (35 ms) echo time, and linear summation of the resulting images. The whole brain was covered (field of view 240x240mm, resolution matrix 80x80 for the *Social - Person Knowledge Task* and 80x79 for the *Episodic Task*, reconstructed voxel size of 3mm and slice thickness of 4mm) with a tilt of 45° off the AC-PC line to reduce the effect of ghosting in the temporal lobe. The flip angle was 85° and the TR was 2.8.

The *Social -Theory of Mind* dataset was acquired using the HCP stage 2 protocol, described in full in Uğurbil et al., (2013). In brief, the use of highly-accelerated, multiplexed, multi-banding EPI (Feinberg et al. 2010; Moeller et al. 2010; Setsompop et al. 2012; Xu et al. 2012) allowed a high spatial resolution (2.0 mm isotropic voxels) with a low TR (720 ms). The whole-brain image was acquired on a modified 3T Siemens Skyra with a 32 channel head coil (multi-band acceleration factor = 8, TE = 33.1 ms, flip angle = 52°, field of view = 208 × 180 mm, 72 slices). One run was acquired with a right-to-left phase encoding and the other with a left-to-right phase encoding, to help factor out the effect of phase encoding direction.

Episodic Task Data

The *Episodic Task* data were previously reported in a univariate assessment of the role of inferior parietal regions in episodic and semantic memory (Humphreys et al. submitted). The dataset was event-related and included episodic retrieval, semantic retrieval, semantic decision and visual (scrambled pattern decision) control conditions. The episodic retrieval task involved retrieving specific features of photographs presented prior to entering the scanner. Outside of the scanner participants were presented with a colour photograph of an object or scene for ten seconds and required to describe it aloud. Within the scanner, a question was presented referring to the previously seen object, for instance, 'What colour was the balloon?'. Two potential answers were presented alongside the question (e.g., 'Blue' and 'Green'). A scrambled photo was also present on screen, but was not relevant to the performance of the episodic task. Participants reported the vividness of their memory on each trial on a scale from 1 to 4. Each episodic trial lasted 4 seconds. The visual control task involved a judgement of whether a scrambled photograph was on the left or right of the screen. There were three task runs each lasting 621.6 seconds and including 222 volumes. The task model included episodic, semantic retrieval, semantic decision, visual control, rest and instruction events. However, only the episodic and control conditions are

of critical interest here as only these conditions attest to the proposed role of the DMN in episodic processing.

Social - Person Knowledge Task Data

The data used to assess the role of the DMN in person knowledge were reported previously ('Study 1' in Rice et al. (2018)). In the original study, only univariate analyses were performed and the focus was the selectivity of social concepts (including multimodal person knowledge) within the anterior temporal lobes and not to probe the DMN. Participants performed the same semantic judgement ('Is the stimuli European/not?') on 3 different categories of stimuli (people, landmarks and animals) presented in either the auditory domain (as spoken words) or the visual domain (as pictures). Visual and auditory control conditions were created by scrambling the images and phase-scrambling auditory tones. Participants were asked whether the image was high or low on the screen or if the auditory tone was high or low-pitched. The *Social - Person Knowledge* task data were acquired over three 12 minute runs, each including 255 dynamic scans (including 2 dummy scans to be removed). Stimuli were presented in blocks of 18 seconds. Social (faces and names), non-social (auditory or visual presentation of landmarks and animals), control (visual and auditory baselines) and rest conditions were included in the task model. All contrasts included equal numbers of trials presented in the auditory and visual domains.

Social - Theory of Mind Task Data

The *Social - Theory of Mind* data were downloaded from the HCP website (Van Essen et al. 2013). Full details of the task design are provided in Barch et al., (2013). Frith-Happe animations were taken from previous studies (Castelli et al. 2000; Wheatley et al. 2007) and, where necessary, shortened to a 20 second duration. These animations consist of moving shapes, which either move randomly or appear to interact with each other in a way that takes into account the other shapes thoughts and feelings. On each trial, participants viewed a social or random motion video

for 20 seconds and were required to assess whether the shapes had an interaction of a social nature. Participants then responded that the shapes had a social interaction, did not have an interaction, or that they were not sure, in an additional 3 second window. This 23 second duration was treated as one block and 5 task blocks (mixed between social and random conditions) were presented with 5 fixation blocks in each of the 2 runs. Each run lasted 3 minutes and 27 seconds (including an 8 second task initiation period) and contained 274 volumes. The task model included social and non-social conditions, as well as rest. This task was chosen for the HCP as it gives reliable and robust activations across participants in univariate analyses and is considered an objective test of theory of mind processes (Castelli et al. 2000; Castelli et al. 2002; Wheatley et al. 2007; White et al. 2011; Barch et al. 2013). This is therefore an exemplary dataset in which to assess the role of the DMN in theory of mind processes.

Preprocessing Methods

The *Episodic* and *Social - Person Knowledge* data were processed using a pipeline based on Jackson et al., (2019), involving the use of statistical parametric mapping (SPM 8) software (Wellcome Trust Center for Neuroimaging) and the Data Processing Assistant for Resting State fMRI (DPARSF Advanced Edition, V2.3) toolbox (Chao-Gan et al. 2010). This pipeline is based on resting-state processing and is designed to remove a substantial proportion of the effects of motion. However, unlike the resting-state processing, the global mean was not removed from the data and the data were not filtered, as these steps may change the relation between the activity of an area and the task model. The steps performed included slice time correction, realignment, coregistration, removal of motion and tissue-based regressors, normalisation using DARTEL and linear detrending. The tissue-based regressors included the average activity in the cerebrospinal fluid and the white matter. The motion regressors employed were the Volterra-expanded 24 motion parameters (Friston et al. 1996) and high motion time points identified using the ARtifact detection Tools software package (ART;

www.nitrc.org/projects/artifact_detect). High motion trials were removed. If removal of high motion trials resulted in the exclusion of more than a quarter of the remaining data then the participant was removed. This resulted in the removal of one participant in the social dataset and none in the episodic dataset.

The pre-processed *Social - Theory of Mind* data were downloaded from the HCP website (http://www.humanconnectomeproject.org/data/; Van Essen et al. 2013). The HCP processing pipeline is described in more detail in Glasser et al., (2013). The pipeline relies upon tools from FSL (Jenkinson et al. 2012) and FreeSurfer (Fischl 2012). The key steps are gradient unwarping, FLIRT-based motion correction, TOPUP-based distortion correction using the fieldmap, brain-boundary-based registration of the EPI data to the structural scan, non-linear (FNIRT) registration into MNI152 space, grand-mean intensity normalization and bias field removal. This process requires skull-stripping and segmentation of the structural scan using FreeSurfer. All data had to pass quality control checks to be included in the HCP dataset (see Marcus et al. 2013) and only those without issues identified were included in the present study. The resulting data are therefore, fully-processed high quality EPI data in MNI atlas space with care taken to minimise the effects of participant movement and distortion. As no overt smoothing had been performed on the downloaded images, smoothing was performed using a 4 mm full-width half maximum (FWHM) Gaussian kernel, following Barch et al., (2013).

Independent Component Analyses

In order to determine the coherent networks present, a separate group ICA was performed on each task dataset. ICA was performed using the Group ICA of fMRI Toolbox (GIFT; Calhoun et al. 2001). The number of components within the data was estimated within GIFT using the group mean Minimum Description Length criteria (Li et al. 2006). The ICA was set to discover this number of components, deemed appropriate for the dataset. Each component comprises a

spatial map and a time-course of activation. The resulting components are presented as group-level spatial maps, calculated by performing a one sample t-test on all the individuals' data to identify voxels that are significantly active across individuals. This may be performed using the utilities provided within GIFT and results in a standard statistical map for each component which was thresholded at a voxel-level significance threshold of .001 and an FWE-corrected critical cluster level of .05. Artefactual components were identified visually based on the spatial map of each component in the same manner as Jackson et al., (2019) and in line with published guidelines (Griffanti et al. 2017). This entailed removal of components with activity focussed outside of the grey matter (whether it be within the ventricles, white matter or outside the brain) or in the brain stem. When removing artefactual components, the researcher was blind to the correspondence of the components with the network templates and the task model. These artefactual components were excluded from further analyses.

Identifying the Coherent Networks in the Task Data

To ensure an accurate reflection of the consensus in the literature, two *a priori* templates were used to determine the component or components corresponding to the DMN in each task dataset; the DMN identified in the resting-state dataset in Jackson et al., (2019) and a publically available DMN template (http://findlab.stanford.edu/functional_ROIs.html; Shirer et al. 2012). The two templates were used independently to identify the DMN and their results compared. Identification of the DMN followed the same procedure as in Jackson et al., (2019). The Jaccard similarity coefficient (Jaccard 1912) was computed between a binarised map of the areas significantly active in the component at the group level and the binary templates. This gives a single measure of template fit that accounts for both extra and missing areas compared to the template, ranging from 0 (no overlap of active voxels) to 1 (full overlap of both active and inactive voxels). As in Jackson et al., (2019), a two-step procedure was employed, firstly allowing all components that reach a threshold of $J = 0.15$ to be identified and then assessing whether

combining multiple components numerically improves the template fit. Unlike the sole use of a threshold, this two-step process allows identification of all components that may be related to the template and then clarifies whether multiple components are the best fit for the network (e.g., if the network has split) or if a single component is a better fit (e.g., there is only one DMN component and a distinct but spatially overlapping network).

Testing the Function of the Coherent Default Mode Network

The function of the coherent DMN can then be assessed by comparing the time course of the identified DMN component(s) to the task model. The beta coefficients were extracted per condition, based on the SPM design matrix. A one-way ANOVA with condition as the factor was used to assess whether the activity in a specific component related to the task model. Planned contrasts were implemented if the task model was significant. In each task a critical comparison was used to determine whether the DMN was involved in the condition of interest (*Episodic Task;* episodic>control; *Social - Person Knowledge;* social (visual faces and auditory names)>non-social (visual and auditory animals and landmarks); *Social - Theory of Mind;* social (intentional) >non-social (random) motion). All tasks were plotted against rest. Bonferroni correction was applied for the resulting three planned contrasts each for the *Episodic Task* and the *Social - Theory of Mind Task*. For the *Social - Person Knowledge* data, it would be possible to find no difference between the social and non-social semantic conditions because of involvement of the coherent DMN in both social and non-social semantics. Therefore, this possibility is assessed by additionally contrasting the social and non-social conditions to a non-semantic baseline. For this dataset Bonferroni correction was applied for six planned contrasts. The Bonferroni-adjusted p-values are reported in all cases.

The main focus of this paper is to test hypothesised functions of the network-of-interest, the DMN. Therefore the full pattern of results is shown for the network-of-interest. However, these

findings may be complemented with an understanding of the networks responsible for episodic and social processing. Therefore, all non-artefactual components were checked to assess whether they significantly related to the task model. Of these task-related models, all those that showed significantly greater activity for the task of interest than the critical baseline condition are presented.

Results

Determining the Components in each Task Dataset

Based on the group mean Minimum Description Length criteria estimates, 26 components were identified in the *Episodic Task* dataset, 31 in the *Social - Person Knowledge* dataset and 20 in the *Social - Theory of Mind* dataset. Artefactual components were removed from each dataset (*Episodic Task, 12 artefactual components; Social - Person Knowledge, 17 artefactual components; Social - Theory of Mind, 9 artefactual components).* Components in each dataset are referred to as E (*Episodic Task*), P (*Social - Person Knowledge Task)* or T *(Social - Theory of Mind Task*) followed by their associated number. All non-artefactual components are shown in Supplementary Figures 1, 2 and 3.

Identifying the Network-of-Interest within each Task Dataset

Each non-artefactual component was quantitatively compared to the DMN templates using the Jaccard similarity coefficient. Comparison to the DMN identified in Jackson et al., (2019) detected a single component above threshold in each task dataset (*Episodic Task, E9, J = .209; Social - Person Knowledge, P18, J =.174; Social - Theory of Mind, T8, J =.235).* In the *Social - Theory of Mind Task* two other components had a Jaccard similarity coefficient greater than the initial threshold of .15 (T13; J=.161, T2; J=.157). However, the combination of the first component (T8) with these additional components reduced the similarity with the template, therefore only T8 was selected as reflecting the DMN. The DMN template provided in Shirer et al., (2012) identified the same components (*Episodic Task, E9, J = .191; Social - Person Knowledge, P18, J*

=.158; Social - Theory of Mind, T8, J =.207), confirming successful detection of a DMN consistent with the prior literature. In the *Social - Theory of Mind Task* an additional component reached the initial selection threshold (T13; J=.164), yet combining the two components reduced the similarity with the template, therefore only T8 was selected. Figure 1 shows the overlap between the component identified in each dataset and the Jackson et al., (2019) template. Overlap with the Shirer (2012) template may be seen in Supplementary Figure 4. All identified components include the core DMN regions and their peak activations are listed in Table 1.

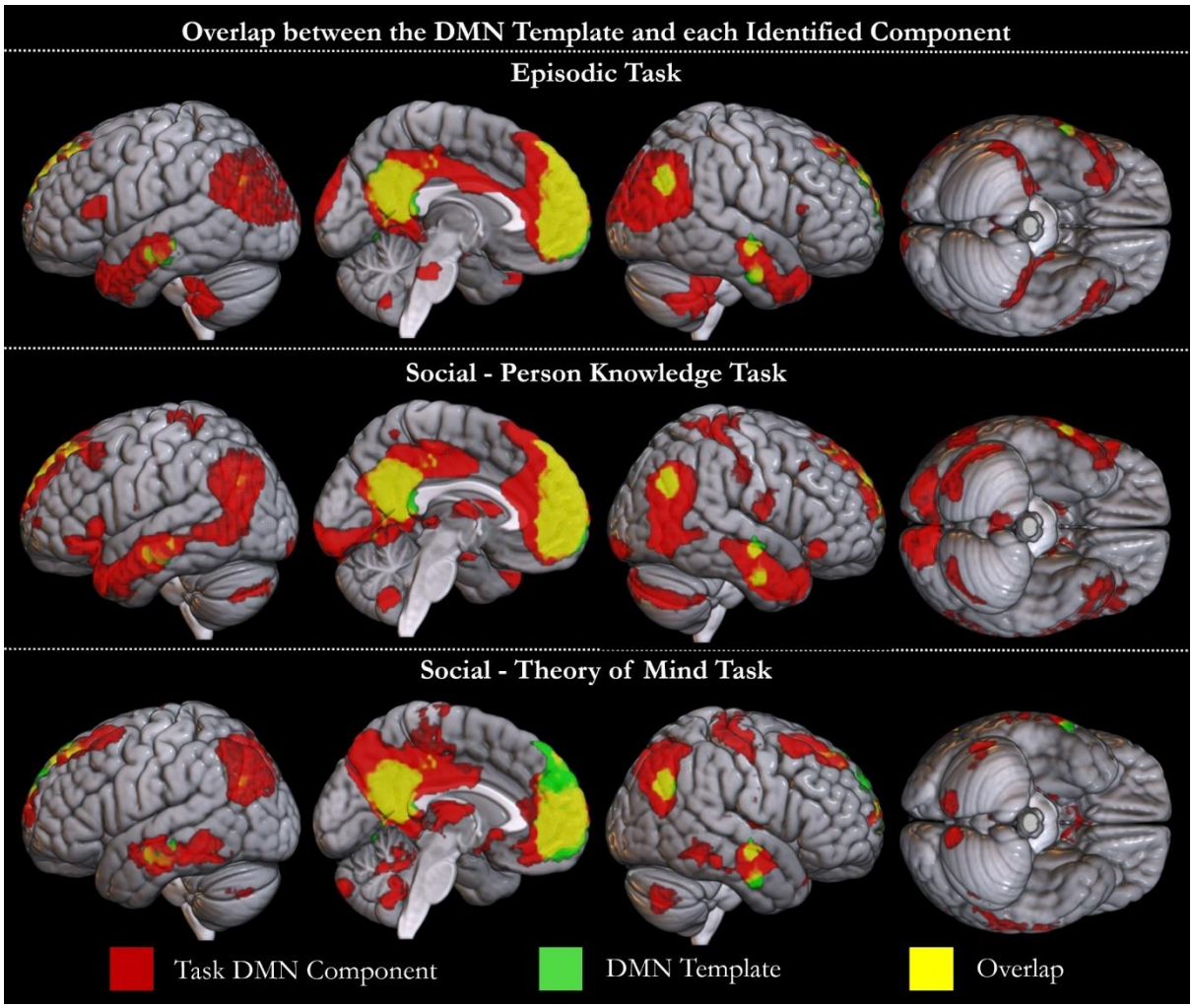

Figure 1. The spatial overlap between the *a priori* template obtained from Jackson et al., (2019) and the component identified to be the DMN in each task is shown. The components identified in the *Episodic Task* (E9), *Social - Person Knowledge Task* (P18) and *Social - Theory of Mind Task* (T8) datasets are shown in red. The template is shown in green. Overlap is shown in yellow.

Testing the Hypothesised Functions of the Coherent DMN

Episodic Task Results

The DMN component (E9) is shown in Figure 2.A. This component was significantly task-related ($F(4, 105)=43.138$, $p<.001$). The critical contrast of episodic > control processing showed significantly less activity in the DMN for the episodic than the control condition ($t(21) = -7.817$, $p<.001$). This provides no evidence for the involvement of the DMN in explicit episodic retrieval tasks. Both the episodic and control condition were deactivated compared to rest, significantly for the episodic condition ($t(21) = -10.249$, $p<.001$) and as a trend for control ($t(21) = -2.431$, $p=.050$). The behavioural profile of the DMN component is shown in Figure 2.A.

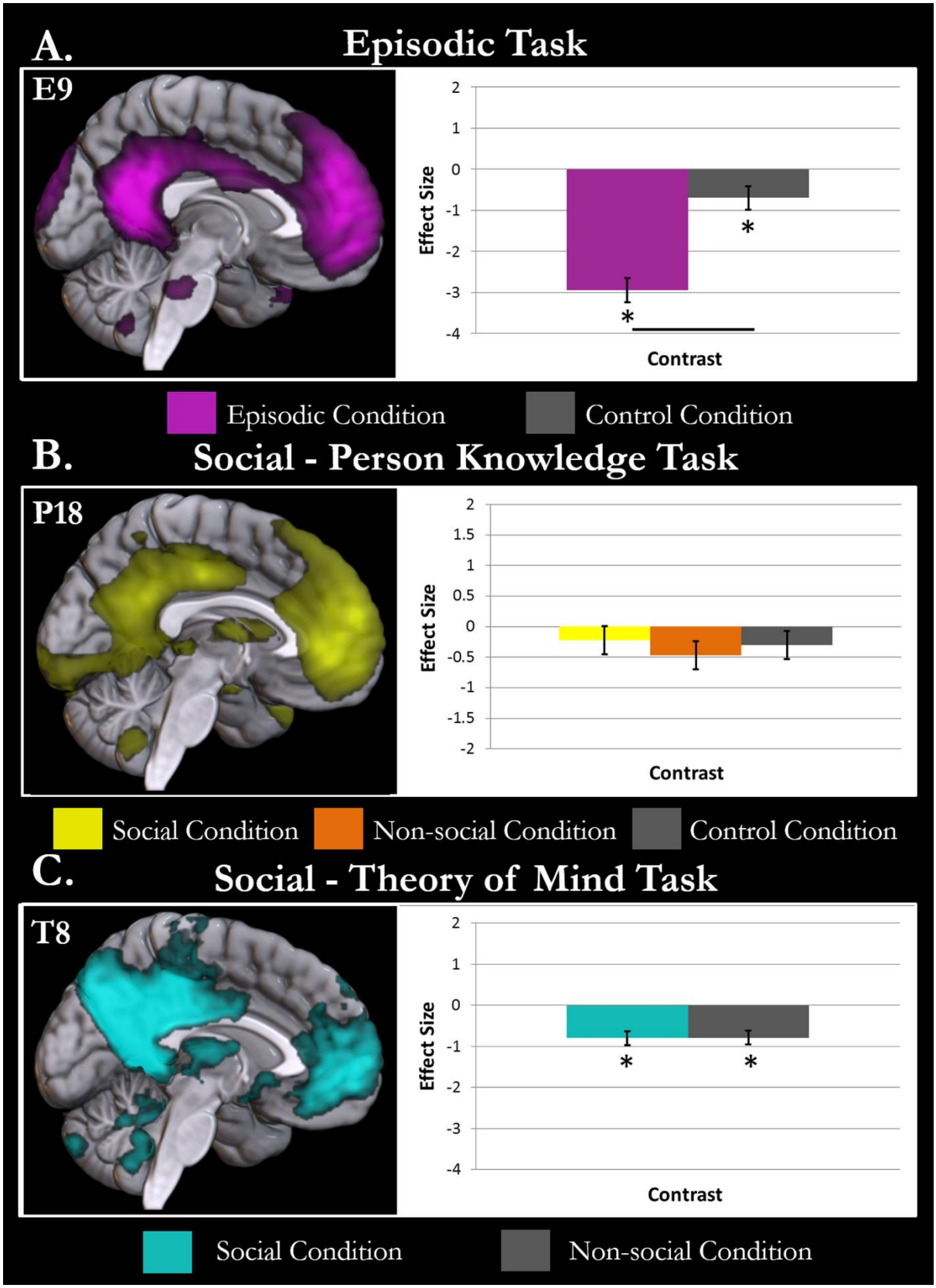

Figure 2. The task relation of the DMN component identified in each task is shown. Conditions with activity significantly different to rest (p<.05 after Bonferroni adjustment) are highlighted with an asterisk. Differences between conditions are demonstrated by a black line between the condition bars. A. The *Episodic Task* DMN component is displayed in violet. The involvement of

the component in the episodic (violet) and baseline conditions (grey) is displayed against rest. B. The DMN component identified in the *Social - Person Knowledge Task* is displayed in yellow. The activity of the component in the social semantic (yellow), non-social semantic (orange) and baseline conditions (grey) are shown compared to rest. C. The DMN component identified in the *Social - Theory of Mind Task* is shown in cyan. The activity of this component in the social motion (cyan) and non-social motion conditions (grey) are shown against rest. The DMN was not found to be significantly more active in the condition of interest (episodic/social processing) than the baseline condition for any task.

To further understand the results of univariate analyses of episodic data, all non-artefactual components with a significant relation to the task model, were assessed for their involvement in episodic processing. The contrast episodic > control processing was significant for components E15, E19, E20 and E25. Each of these components is shown in Figure 3 and the areas of peak activation are listed in Table 2. E15 involved frontal and parietal regions with a left dominance and may reflect the left frontoparietal control network (Vincent et al. 2008). E19 includes a large swathe of dorsomedial prefrontal cortex and anterior cingulate cortex, as well as supramarginal gyrus, frontal and occipital areas. E20 was primarily centred on the precuneus and bilateral angular gyri, the defining features of the precuneus network (Margulies et al. 2009; Uddin et al. 2009). E25 involves activity in occipital, posterior inferior temporal, motor and posterior cingulate cortices, as well as a small region of the medial prefrontal cortex. The full behavioural profile of these components is shown in Figure 3. All were activated for the episodic condition compared to rest (E15; $t(21)= 19.497$, $p<.001$; E19; $t(21)= 9.778$, $p<.001$; E20; $t(21)= 6.017$, $p<.001$; E25; $t(21)= 19.655$, $p<.001$) and all except E15 showed significantly greater activation for the control condition than rest (E15; $t(21)= -2.258$, $p=.078$; E19; $t(21)= 4.663$, $p<.001$; E20; $t(21)= 3.128$, $p<.001$; E25; $t(21)= 16.913$, $p<.01$). This may reflect some (albeit lesser) involvement of these components in the visual task.

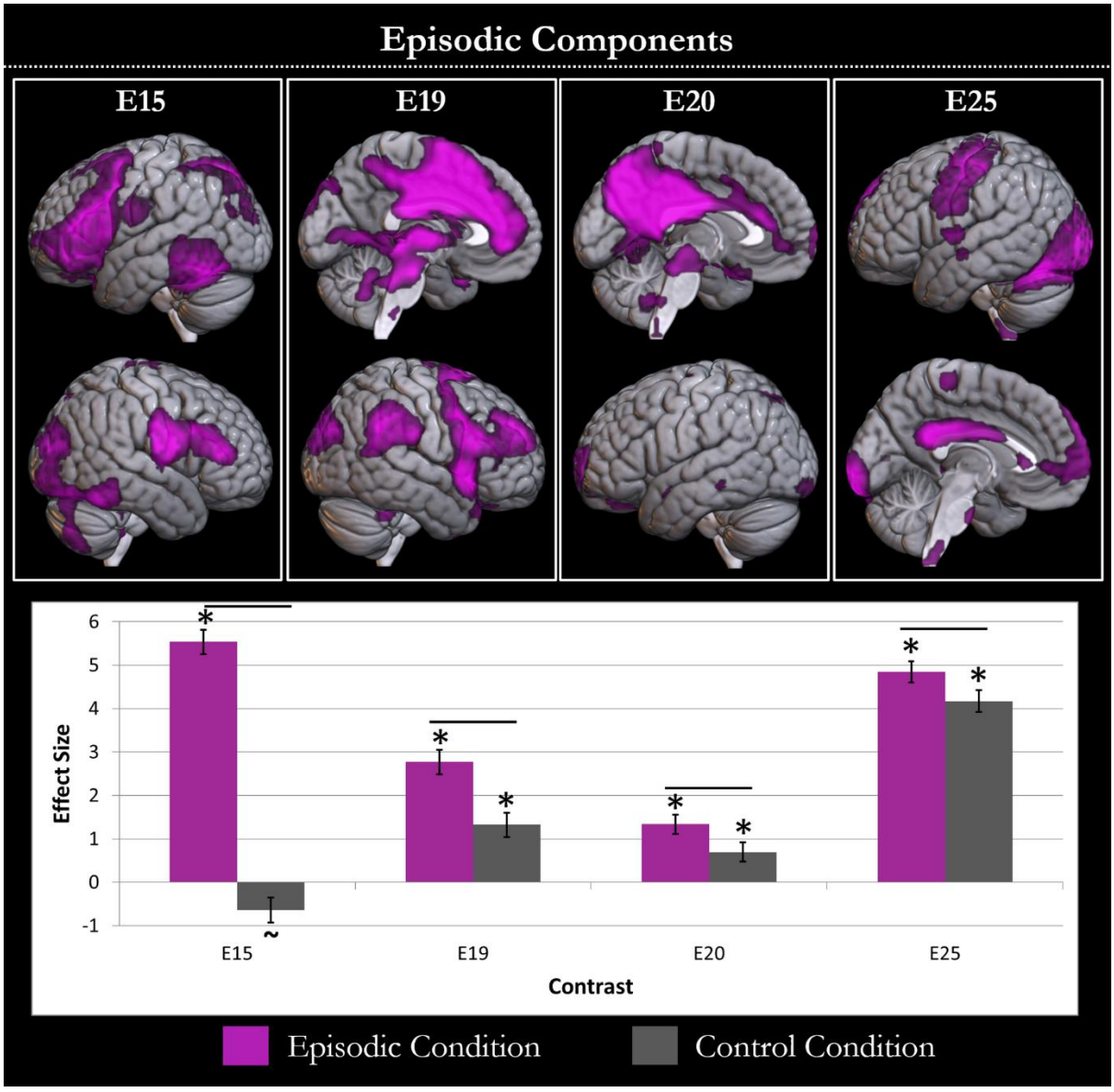

Figure 3. The components with greater involvement in the episodic than the baseline condition are displayed. Each component is shown in violet in the top panel and the task relation of the component is shown in the lower graph. The graph shows the effect size of each component in the episodic (violet) and baseline (grey) conditions compared to rest. Conditions with activity significantly different ($p<.05$ after Bonferroni adjustment) to rest are highlighted with an asterisk. A tilde is shown if there is a trend ($p<.1$ after Bonferroni adjustment) towards this difference. Differences between conditions are demonstrated by a black line between the condition bars.

To aid interpretation of why univariate activation differences may be identified in DMN regions during an episodic task, the spatial extent of the (binarised) combination of components that show an episodic effect was compared to the spatial extent of the (binarised) resting-state DMN, shown in Figure 4. Together the episodic components included a large proportion of the cortex

including almost the entire medial surface. Despite this, the combination of the components shows minimal overlap with the DMN template on the lateral surface, instead appearing anti-correlated. Lateral DMN areas appear to fall between these components (e.g., in lateral temporal cortex), with some areas suggesting differentiable involvement of subregions (e.g., distinct areas of the angular gyrus implicated in the DMN and episodic memory). Whilst much of the medial regions do show overlap, this is the result of distinct episodic components involving the posterior and anterior DMN regions. Overall, these results suggest a key role for multiple networks in episodic cognition, including the precuneus network and left frontoparietal networks. There is no evidence the coherent DMN is involved in episodic retrieval. However, many of the areas in or near the DMN do appear to be involved in episodic memory as part of other (sometimes multiple) networks.

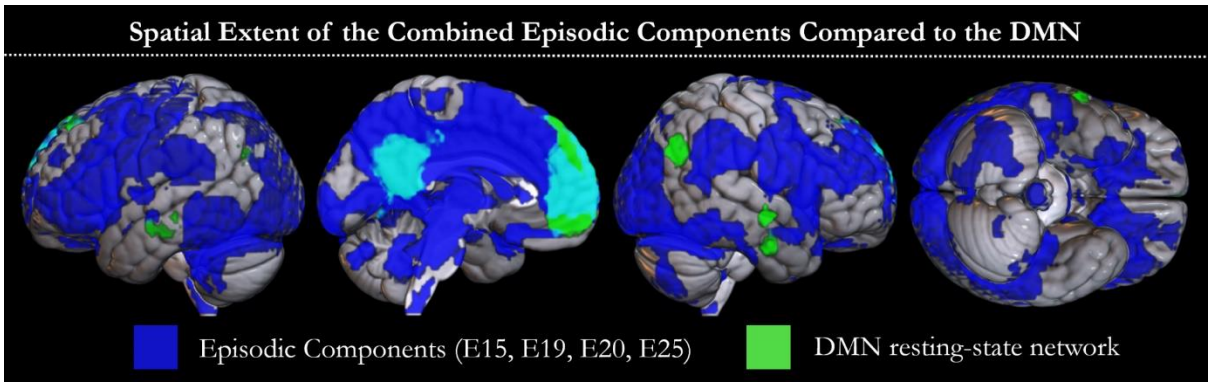

Figure 4. The (binarised) combination of the four components implicated in episodic memory (blue) are overlaid with the (binarised) DMN template identified in the resting-state (green). This shows the spatial distribution of the episodic networks and their overlap with the DMN.

Social - Person Knowledge Task Results

Figure 2.B. shows the DMN component identified in the *Social - Person Knowledge Task* data (P18). The DMN was not significantly task-related ($F(3,68)=1.425$, $p=.243$) therefore the results of the contrasts should not be interpreted. However, for completeness in assessing the core goal of the current endeavour the contrasts are reported here with caution. The contrast social > non-social

was not significant (t(18)=1.074, p=1). These results provide no evidence that the DMN is specifically involved in the kind of social cognition necessary to perform person knowledge judgements. Neither the social or non-social conditions were significantly different to the non-semantic control condition (social>control; t(18) = 0.364, p=1; non-social>control; t(18) = -0.711, p=1). The coherent DMN was not involved in either social or general semantics, providing no evidence that the DMN is necessary for social tasks of this nature. In addition, this independent dataset shows no involvement of the coherent DMN in semantic cognition, supporting the conclusions from Humphreys et al., (2015) and directly replicating the findings of Jackson et al., (2019). Compared to rest, both the social (t(18) = -0.954, p=1) and the non-social condition (t(18) = -2.028, p=.279) show non-significant deactivation of the coherent DMN.

No other components were significantly more active in the social condition compared to the non-social condition, even without correction for multiple comparisons. This does not imply that there were no components involved in the social task, but merely that none were involved to a significantly greater extent when the relevant knowledge was related to people. Indeed, the same components were recruited equally for the social and non-social semantic conditions (P12; F(3,68) = 8.253, p<.001, social *vs.* control t(18)=3.974, p<.005, non-social *vs.* control t(18)= 2.817, p<.05, social *vs.* non-social t(18)=1.157, p=1; P31; F(3,68) = 17.713, p<.001, social *vs.* control t(18)=2.978, p<.05, non-social *vs.* control t(18)= 3.415, p<.01, social *vs.* non-social t(18)=-0.437, p=1). P12 involved bilateral temporal cortices and inferior frontal gyri, areas critical for general semantic cognition. P31 included occipital and motor cortex and may reflect the processing of visual input and motor output. Both are shown in Supplementary Figure 2.

Social - Theory of Mind Task Results

The DMN component (T8) identified in the *Social - Theory of Mind Task* is displayed in Figure 2.C. alongside the activity of the social and non-social conditions (plotted against rest). The DMN

was significantly related to the task model ($F(2,237)=15.297$, $p<.001$). The contrast social > non-social was not significant ($t(79)=-0.047$, $p=1$). Therefore, no evidence was provided for the hypothesis that the DMN is involved in theory of mind. The DMN was deactivated compared to rest for viewing motion with or without social interaction (social>rest; $t(79)=-4.814$, $p<.001$; non-social>rest; $t(79)=-4.766$, $p<.001$).

All non-artefactual components were assessed for their relation to theory of mind processing. One component showed a significant effect for the social > non-social contrast (T10; $F(2, 237)=48.393$, $p<.001$; $t(79)=3.448$, $p<.005$). T10 was significantly activated for both social ($t(79)=9.704$, $p<.001$) and non-social ($t(79)=6.256$, $p<.001$) motion over rest. The spatial extent and behavioural profile of T10 is shown in Figure 5. The locations of peak activations in T10 are recorded in Table 2. T10 is left hemisphere-biased and includes bilateral inferior and middle frontal gyri, dorsomedial prefrontal cortex, inferior parietal lobe and posterior inferior temporal cortex. All regions had a greater extent in the left hemisphere and there was additional involvement of left middle and superior temporal gyri. This component appears to reflect the left frontoparietal control network and is involved in processing both kinds of motion, yet to a much greater extent when processing the social condition. As there is no high-level baseline in this dataset it is not possible to accurately assess the networks involved in both social and non-social conditions. Therefore, no further results are presented.

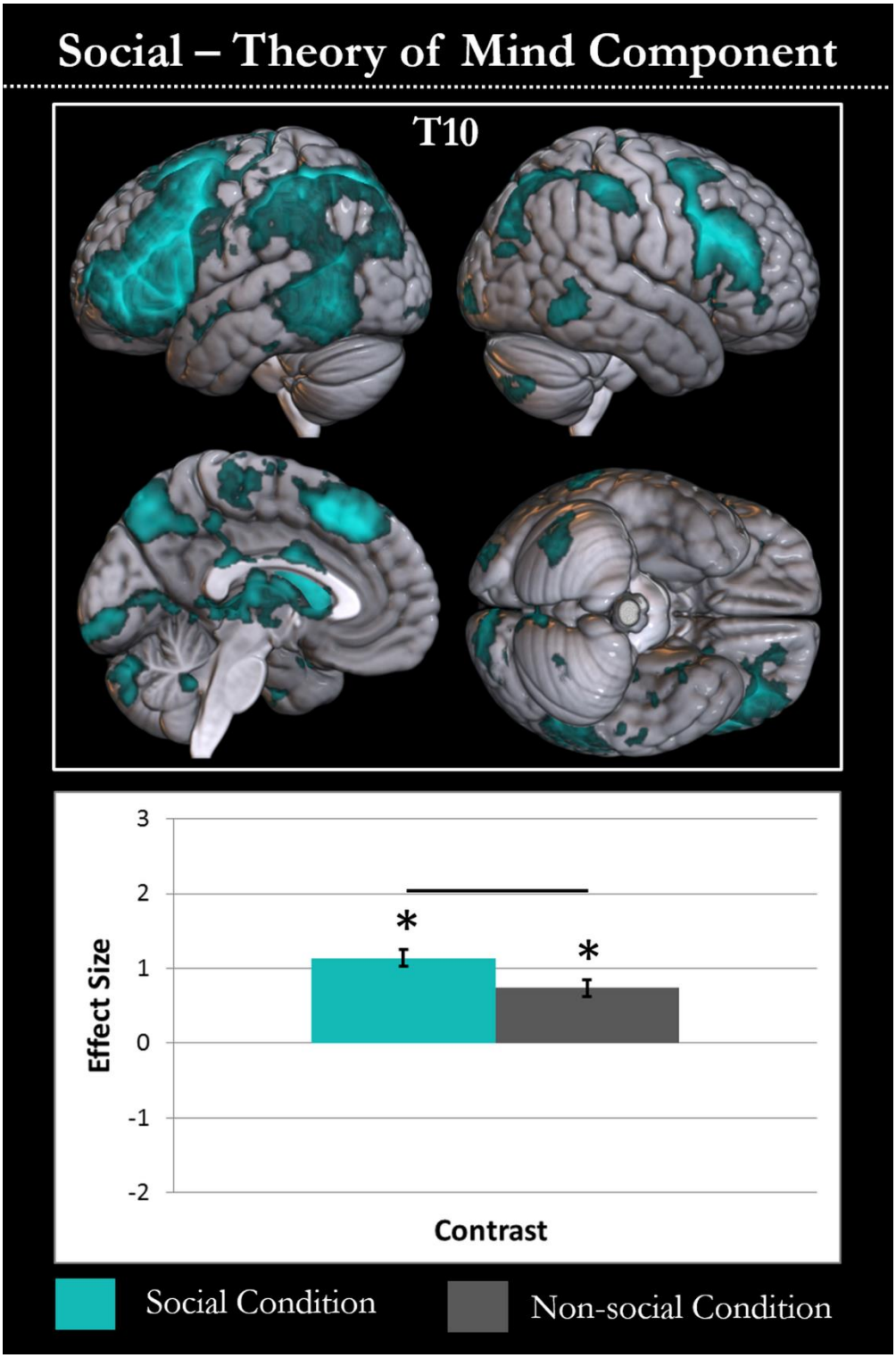

Figure 5. The single component with greater involvement in the theory of mind than the baseline condition is displayed. The spatial extent of the component is shown in cyan in the top panel and the task relation of the component is shown in the lower graph. The graph shows the effect size of each component in the social motion (cyan) and non-social motion conditions (grey) compared to rest. Conditions with activity significantly different ($p<.05$ after Bonferroni adjustment) to rest are highlighted with an asterisk. Differences between conditions are demonstrated by a black line between the condition bars.

Discussion

A network-level approach found no evidence for involvement of the coherent DMN in episodic or social cognition. Indeed, the DMN showed the reverse of the pattern one would expect from an episodic network, being significantly less active in the episodic than the visual baseline task, and all tasks showed less DMN involvement than rest. Additionally, both episodic memory and theory of mind recruited a left-biased frontoparietal network (FPN), typically associated with a task-positive activation pattern and executive control processing (Vincent et al. 2008). The networks implicated in each domain aligned well with the literature. Multiple networks contributed to episodic processing, perhaps supporting different processes. Visual assessment suggests these components include the precuneus network and the left FPN, as well as components focussed on frontal, occipital, cingulate, inferior temporal and motor regions. Whilst traditional episodic memory research focussed on the MTL, there is an increasing trend to accept that multiple distributed areas or networks are involved, including precuneus, angular gyrus and frontal cortex (Buckner et al. 2001; Rugg 2002; Lundstrom et al. 2005; Wagner et al. 2005; Kim 2010; Ranganath et al. 2012; Hirose et al. 2013; Jeong et al. 2015). Person-knowledge relied on the same semantic network as knowledge of non-social concepts, which corresponded extremely well to prior assessments of semantic cognition (Binder et al. 2011; Lambon Ralph et al. 2017), including the lack of involvement of the coherent DMN (Jackson et al. 2019) and its constituent regions (Humphreys et al. 2014; Humphreys et al. 2015; Humphreys et al. submitted). Although univariate comparison may find subtle differences between social and non-social judgements, these are in the wider context of similar networks and may relate to difficulty level (Zahn et al. 2007; Binney et al. 2016; Rice et al. 2018; Binney et al. 2020). In contrast, theory of mind relied on a distinct network, the left FPN, associated with executive processing, planning and information load (Vincent et al. 2008; Spreng et al. 2010; Summerfield et al. 2010; Meyer et al. 2012; Spreng 2012). This is highly compatible with prior analyses of this task,

involving core dorsomedial prefrontal cortex and temporoparietal junction regions areas implicated in mentalising (Castelli et al. 2000; Castelli et al. 2002; Wheatley et al. 2007; Barch et al. 2013). In the remainder of the Discussion, we consider why prior univariate and meta-analytic results have associated the DMN with episodic and social cognition and the implications for the role of the DMN.

Why do regions of the core DMN appear in univariate episodic and social analyses? The coherent DMN was not involved in the episodic or social tasks, however it has been linked to all of these processes previously on the basis of univariate results. There are multiple possible reasons why this may occur and distinct factors may be critical for the different tasks. Many of the constituent regions of the DMN are involved in episodic memory as part of distinct networks, such as the FPN and the precuneus network, consisting of dorsal precuneus and bilateral angular gyri (Damoiseaux et al. 2006; Buckner et al. 2008; Margulies et al. 2009; Stevens et al. 2009; Zhang et al. 2012; Yang et al. 2013; Utevsky et al. 2014). These networks may be separated by ICA (Damoiseaux et al. 2006; Stevens et al. 2009; Zuo et al. 2010) and distinguished on the basis of function (Utevsky et al. 2014), including the relation of their constituent regions to episodic memory (Sestieri et al. 2011). Here we support this distinction by demonstrating that the precuneus network, but not the coherent DMN supports episodic memory. Both the precuneus and the angular gyri are commonly associated with episodic processing (Lundstrom et al. 2003; Lundstrom et al. 2005; Wagner et al. 2005; Cavanna et al. 2006; Cabeza et al. 2008; Dorfel et al. 2009; Humphreys et al. 2014), yet whether this was due to the activity of the core DMN or precuneus network was not previously clear. Overlap with other networks, alongside a lack of precision in the definition and identification of the DMN, may have led to the association of the DMN with episodic memory. Additionally, when multiple networks are implicated in a task, perhaps engaging overlapping regions in different ways, measures of the sum activity in a single region may be difficult to

interpret without network-level assessments. This may be exacerbated by difficulty differences or by being at the edge of multiple partially overlapping networks.

Difficulty differences leading to relatively greater time spent in free thought during a trial may be a critical factor in prior analyses of social versus non-social semantics. Whilst these conditions do not vary at a network level, relative differences could be induced (within the semantic network engaged in the task and the DMN deactivated during the task) via easier items or tasks (Spreng 2012; Humphreys et al. 2017). Alternatively, the critical issue may be the accurate identification of DMN regions. Meta-analyses of theory of mind have shown involvement of DMN regions (particularly medial prefrontal cortex), however the focus may be outside of core DMN regions (e.g., temporoparietal junction; Buckner et al. 2008; Van Overwalle 2009; Mars et al. 2012) and explicit overlap is minimal (Mars et al. 2012). This highlights the importance of assessing function at the network-level approach.

How do these network-based results fit with the classical deactivation-based definition of the DMN? It is important to consider how these assessments of the coherent DMN relate to the wider set of regions showing greater activation in rest than many tasks (regardless of connectivity or co-activation). As well as the coherent DMN, this pattern may be found for the precuneus and semantic networks identified as task-related here, likely due to the high propensity for episodic and semantic cognition during rest (Humphreys et al. 2015). Each of these networks were separated based on their connectivity and had distinct cognitive profiles. This supports a componential view of these task-negative regions, suggesting they do not reflect one coherent network, but multiple component parts with dissociable functions, such as episodic, social and semantic cognition (e.g., Andrews-Hanna et al. 2010; Leech et al. 2011; Spreng 2012; Humphreys et al. 2015; Axelrod et al. 2017). Indeed, most regions may deactivate in the correct task context; even primary sensory regions deactivate when other senses are engaged (e.g., Humphreys et al.

2015). Varying the task contexts used to construct a network of task-deactivated regions, can result in radically different 'default mode networks' (Callard et al. 2012; Humphreys et al. 2015). In univariate analyses many of the network identified here would deactivate from rest in most (commonly studied) task contexts, and in some connectivity-based analyses these networks may be hard to distinguish from the core DMN due to the correlation caused by their mutual deactivation from rest in many tasks (Humphreys et al. 2015; Jackson et al. 2019). Unlike parcellations of the DMN (e.g., Andrews-Hanna et al. 2010), the variety of networks implicated here are able to include regions outside of the DMN and may have overlapping regions or graded divisions. However, it is critical to separate these constituent networks; simply stating that the set of task-negative regions are responsible for all of these functions is not sufficient. Distinct subsets of these regions, in combination with some additional regions (including task-positive areas), are engaged in distinct tasks. In contrast, a componential approach could explain the relation between the activation, connectivity and function of much of these higher-level cortical regions. However, a coherent DMN was identified in all datasets and not found to be responsible for any of the hypothesised processes. Therefore, there is still a critical question to allow a full picture of these task-negative regions and networks; what function does the coherent DMN support?

What is the function of the coherent DMN? If the coherent DMN is not engaged in episodic, social or semantic cognition what is its functional role? It is possible that this core DMN forms a distinct ICA component without being a coherent network with a function, purely as it is a useful way to explain a lot of variance in the datasets. However, this seems unlikely due to the strong structural and functional connectivity between the core midline regions (which is not explained by the other networks identified) and the extremely high level of consistency in finding the DMN in different task and rest datasets (e.g., Greicius et al. 2009). One possibility is the DMN simply performs some specific episodic or social process not tested here, for instance, episodic memory

encoding, self-referential thought or processing highly emotional stimuli. An important caveat of the current work if that only one episodic task probing recall was used and the involvement of different networks may shift between differentiable episodic subprocesses (Hirose et al. 2013; Jeong et al. 2015). The current study has served to test the simple hypothesis that the core DMN is involved in all episodic tasks and found no evidence in favour of this theory. However, further testing of the coherent network may find evidence supporting a more specific role. Alternatively, it may be that this core DMN uses information provided by the semantic and episodic networks, yet their combination is more than the sum of its parts. For instance, distinct combinatorial processes may be required to produce a train of thought (Humphries et al. 2007; Graves et al. 2010; Price et al. 2015) or additional mental simulation may be needed to imagine the future using past events (Buckner et al. 2007; Binder et al. 2011). The core DMN may work in concert with related networks to use episodic and semantic information in a complex manner (Irish et al. 2013). Alternatively, the DMN may be responsible for processing in a different domain that we have yet to consider. To determine this, the relationship between the coherent DMN and various different task processes should be assessed using a network-level approach.

An alternative possibility is that whilst associated networks, such as the precuneus and semantic networks, may simply perform some process that is more common in rest than across the typical explicit tasks used for comparison, the coherent DMN is not responsible for processing in a specific domain. Instead DMN activation may signify a change in attentional processes. The DMN may reflect internally-directed attention (Andrews-Hanna 2011; Smallwood et al. 2013; Scheibner et al. 2017) or mind-wandering and 'off-task thoughts' (McKiernan et al. 2006; Smallwood et al. 2006; Mason et al. 2007). These task-unrelated thoughts are not considered to be entirely explicable based on the function of base systems but require additional unique processes (Smallwood et al. 2012; Seli et al. 2018). From these kinds of attentional perspectives, no explicit task could evoke the kind of processes the DMN performs although it is possible to

relate self-reported or boredom-induced mind-wandering to network activity (Smallwood et al. 2006; Christoff et al. 2009). However, these conditions increase the overall amount of off-task thought, therefore a concomitant increase in DMN involvement could reflect any functional process frequently performed during rest. Therefore, it is not clear how this kind of theory may be contrasted with other views of the DMN function and, in the limit, these types of theory may be unfalsifiable (Christoff et al. 2018). Some evidence against the view that explicit tasks cannot activate the DMN is provided in a small amount of prior research linking the DMN to active task processes (Crittenden et al. 2015; Vatansever et al. 2015).

Alternatively, the assumptions adopted to simplify the interpretation of brain networks may not be appropriate for the coherent DMN. For instance, the current study adopted the popular assumption that greater activity (or a higher BOLD signal) in an fMRI study means an area (or network) is more engaged in a task. Whilst this was critical in testing specific hypotheses arising from evidence dependent on this assumption, for a wider interpretation of the coherent DMN role this assumption may be questioned. It may be that the total activity in the DMN remains stable, yet the pattern of activity across the network changes meaningfully, or that deactivation of the DMN may reflect greater engagement of inhibitory processes (Daselaar et al. 2004; Humphreys et al. 2014; Knapen et al. 2018). Currently there are many possible explanations of the function of the DMN. Until this puzzle is resolved, satisfactory interpretations of relevant research, including clinical implications, will not be possible. Therefore, determining the functional role of the coherent DMN through formal network-level hypothesis should be a central focus for research.

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Table 1. Peak activation in the DMN component-of-interest in each task dataset. Voxels are significant at .001. Clusters are significant using FWE-correction and a critical cluster level of 0.05.

Task (Component)	Cluster Region	Cluster extent (voxels)	Max z value	P value (FWE corrected)	Peak MNI Coordinate		
					X	Y	Z
Episodic (E9)	Bil PCC, ACC, mPFC, MFG, precuneus, PHG, hippocampus, FG, cerebellum	7648	> 8	< .001	-3	-54	27
	Bil IPL, P temporal, mid and superior occipital	2807	> 8	< .001	48	-72	36
	L lateral ATL, TP, IFG	830	6.74	< .001	-63	-9	-15
	R lateral ATL	613	6.53	< .001	69	-9	-12
	L insula	474	5.84	< .001	-39	-15	24
	R insula, IFG	509	5.71	< .001	42	-24	21
	R IFG	59	5.10	.038	39	36	-12
	Brainstem	81	4.93	.010	-3	-33	-30
	Cerebellum	64	4.11	.028	-6	-60	-48
Social - Person Knowledge (P18)	Bil mPFC, ACC, MFG	5241	> 8	< .001	6	39	3
	L IPL, P temporal, mid occipital, MTG, TP, IFG, insula	2318	> 8	< .001	-51	-60	27
	Bil PCC, precuneus, occipital, L thalamus, putamen	4273	> 8	< .001	0	-21	39
	R IPL, P temporal, mid occipital	888	7.48	< .001	54	-60	27
	R PHG, hippocampus, insula, IFG, lateral ATL	1146	6.88	< .001	24	-18	-18
	R PCG, SMG, SPL	1155	6.76	< .001	57	-18	36
	L PCG, SMG	691	6.20	< .001	-45	-18	39
	Cerebellum	239	5.80	< .001	-27	-81	-36
	Cerebellum	239	5.15	< .001	6	-54	-45
	R putamen, insula, HG	138	5.09	< .001	33	-24	6
Social - Theory of Mind (T8)	Bil PCC, ACC, precuneus, PL, PHG, FG, cerebellum, R PCG	27834	> 8	< .001	0	-64	32
	L MFG, SFG	1739	> 8	< .001	-20	34	44

Cerebellum	629	> 8	< .001	40	-66	-40
R MFG, SFG	1342	> 8	< .001	24	30	48
R lateral ATL, MTG	1255	> 8	< .001	58	-6	-14
R IFG	170	> 8	< .001	34	36	-10
Cerebellum	136	7.76	< .001	-10	-86	-38
Cerebellum	187	7.67	< .001	10	-84	-36
L lateral ATL, MTG, PITC	1511	7.24	< .001	-60	-46	-8
L IFG	164	6.59	< .001	-32	36	-10
Cerebellum	215	6.43	< .001	-38	-72	-38
R STG	133	4.84	< .001	56	-8	6
R superior TP	81	4.73	.001	38	22	-22

L = left, R = right, Bil = bilateral, P = posterior, A = anterior, CC = cingulate cortex, mPFC = medial prefrontal cortex, IFG= inferior frontal gyrus, MFG = middle frontal gyrus, SFG = superior frontal gyrus, PHG = parahippocampal gyrus, FG = fusiform gyrus, MTG = middle temporal gyrus, STG = superior temporal gyrus, ITC = inferior temporal cortex, ATL = anterior temporal lobe, HG = Heschl's gyrus, TP = temporal pole, CG = central gyrus, SMG = supramarginal gyrus, SPL = superior parietal lobe, IPL=inferior parietal lobe, PL = paracentral lobule.

Table 2. Peak activation in the components identified with each contrast-of-interest. Voxels are significant at .001. Clusters are significant using FWE-correction and a critical cluster level of 0.05.

Contrast	Component	Cluster Region	Cluster extent (voxels)	Max z value	P value (FWE corrected)	Peak MNI Coordinate		
						X	Y	Z
Episodic Task - Episodic > Control	E15	Bil occipital, PITC, IPL, FG, L SPL, PHG, cerebellum, R postCG, IFG, MFG, SFG, preSMA, putamen	19178	> 8	< .001	-30	-63	45
		Bil PL	217	4.59	< .001	6	-24	63
	E19	Bil precuneus, CC, SMA, MFG, IFG, mPFC, preCG, SMG, P temporal, TP, occipital, thalamus, putamen, cerebellum	20012	> 8	< .001	42	21	3
		L occipital, FG, cerebellum	989	7.28	< .001	-33	-39	-24
	E20	Bil precuneus, CC, AG, PMTG, frontal pole, L preCG, PCG	11681	> 8	< .001	9	-45	24
		L inferior occipital	285	6.68	< .001	-21	-93	-9
		R inferior occipital	296	6.45	< .001	21	-90	-9
		R ITG	487	6.40	< .001	57	-21	-33
		Cerebellum	435	6.21	< .001	30	-69	-60
		Brainstem	327	5.52	< .001	3	-30	-21
		R hippocampus, PHG	70	5.27	.022	24	-36	-3
	E25	Bil PITC, occipital, SPL, PCC, PCG, PL, R hippocampus, PHG, thalamus, L STG	11501	> 8	< .001	-36	-60	-15
		R hippocampus, PHG, thalamus	489	6.52	< .001	-27	-30	-6
		Brainstem	59	5.95	.036	-3	-51	-69
		Brainstem	69	4.96	.019	-9	-15	-33
Theory of Mind Task -	T10	Bil preSMA, precuneus, L IFG, MFG, SFG, preCG, IPL, MTG, superior TP, PITC, mid occipital, insula	40653	> 8	< .001	-46	8	34
		R IFG, MFG, preCG	3870	> 8	< .001	52	32	22

Social > Non-social	R IPL, mid occipital	2808	> 8	< .001	36	-54	44
	R insula, IFG	279	7.76	< .001	38	22	-2
	Cerebellum	218	7.34	< .001	-32	-70	-50
	R posterior ITC	1354	7.09	< .001	60	-48	-6
	L mid CC	247	6.95	< .001	-2	2	30
	Cerebellum	81	6.37	.001	2	-52	-34
	R IFG	121	5.92	< .001	34	38	-10
	Cerebellum	149	5.89	< .001	-38	-66	-28
	Bil PCC	192	5.85	< .001	-2	-30	28
	Bil precuneus	483	5.8	< .001	18	-58	18
	R FG	89	5.22	< .001	42	-12	-28
	R mid occipital cortex	48	4.93	.028	46	-82	22
	L putamen	66	4.72	.004	-24	2	-10
	R inferior occipital cortex	209	4.64	< .001	28	-100	0
	R preCG	70	4.56	.003	22	-24	74

L = left, R = right, Bil = bilateral, P = posterior, A = anterior, CC = cingulate cortex, mPFC = medial prefrontal cortex, IFG= inferior frontal gyrus, MFG = middle frontal gyrus, SFG = superior frontal gyrus, PHG = parahippocampal gyrus, FG = fusiform gyrus, ITG = inferior temporal gyrus, MTG = middle temporal gyrus, STG = superior temporal gyrus, ITC = inferior temporal cortex, TP = temporal pole, CG = central gyrus, SMA = supplementary motor area, SMG = supramarginal gyrus, SPL = superior parietal lobe, AG = angular gyrus, IPL=inferior parietal lobe, PL = paracentral lobule.