

Available online at www.sciencedirect.com

ScienceDirect

Journal homepage: www.elsevier.com/locate/cortex

Special Issue “Understanding Others”: Research Report

Cross-network interactions in social cognition: A review of findings on task related brain activation and connectivity

 Matthias Schurz ^{a,b,*}, Lara Maliske ^{c,1} and Philipp Kanske ^{c,d}
^a Donders Institute for Brain, Cognition, and Behaviour, Radboud University Nijmegen, Nijmegen, the Netherlands

^b Wellcome Centre for Integrative Neuroimaging, Department of Experimental Psychology, University of Oxford, Oxford, United Kingdom

^c Clinical Psychology and Behavioral Neuroscience, Faculty of Psychology, Technische Universität Dresden, Dresden, Germany

^d Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

ARTICLE INFO

Article history:

Received 11 August 2019

Reviewed 06 April 2020

Revised 6 April 2020

Accepted 13 May 2020

Published online 22 May 2020

Keywords:

Between-network

Across-network

fMRI

Resting-state

Theory of Mind

Mentalizing

Empathy

Action observation

Connectivity

ABSTRACT

Theory of Mind, empathy, and action observation are central themes in social neuroscience research. Meta-analyses of functional neuroimaging studies show substantial heterogeneity in brain activation for these cognitive abilities, depending on the type of experimental task used. We followed up on these findings by a comparison to basic connectivity networks of the brain. In particular, we evaluated to what extent brain activation for social cognition tasks draws on areas of different fMRI resting-state networks (e.g., Default Mode, Ventral Attention Network) in parallel. Our review illustrates high prevalence of such network co-recruitments across Theory of Mind, empathy, and action observation tasks. To characterize these observations in more detail, we additionally conducted a literature review of fMRI effective connectivity studies. Findings reveal two main types of cross-network interactions in social cognition tasks: Negative coupling (segregation) between Default Mode and Control Networks (Ventral Attention, Frontoparietal, and Dorsal Attention Network), and positive coupling (integration) between these networks. The two patterns reflect different types of brain network organization taking place in the context of social cognition tasks—segregation for specialized, versus integration for flexible processing. We discuss evidence from connectivity research in other research fields, suggesting that increased network integration indicates more effortful and controlled processing. Based on that, we consider how findings of network segregation versus integration can provide new perspectives on dual-system accounts of social cognition, which differentiate between automatic and controlled processes. Moreover, we discuss how the reviewed evidence relates to neural processes which are assumed to take place during naturalistic social cognition.

© 2020 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

* Corresponding author. Donders Institute for Brain, Cognition, & Behaviour, Radboud University Nijmegen, Montessorilaan 3, 6525, HR Nijmegen, the Netherlands.

E-mail address: matthias.schurz@gmail.com (M. Schurz).

¹ These authors contributed equally.

<https://doi.org/10.1016/j.cortex.2020.05.006>

0010-9452/© 2020 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Successful social interactions require representing the mental states of others, such as their thoughts, emotions, and goals. Over the last two decades, neuroimaging research has sought to delineate how the brain enables such representations of information about other minds. In particular, three topics have been highly popular and subject of hundreds of published neuroimaging studies. The first topic, often referred to as Theory of Mind or mentalizing, covers research on how we represent cognitive states of others, such as their thoughts and beliefs (e.g., Adolphs, 2009; Kanske, 2018; Keysers & Gazzola, 2009; Premack & Woodruff, 1978). Second, empathy research has studied how more affective states of others are represented (Gallese, 2003; Jackson, Meltzoff, & Decety, 2005; Singer et al., 2004; Titchener, 1909). While both aforementioned topics feature representations of internal mental states, a third research theme has focused on processes underlying action observation and imitation (Buccino et al., 2004; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Some of these processes have been linked to the “mirroring” of actions, which facilitates understanding of others' goals (e.g., Fabbri-Destro & Rizzolatti, 2008; Gallese & Goldman, 1998; Rizzolatti & Craighero, 2004).

Over recent years, neuroimaging meta-analyses have increased our knowledge of these processes, and systematically investigated the consistency of brain activation across different types of tasks used for studying Theory of Mind (e.g., Molenberghs, Johnson, Henry, & Mattingley, 2016; Schurz, Radua, Aichhorn, Richlan, & Perner, 2014), empathy (e.g., Fan, Duncan, de Greck, & Northoff, 2011; Timmers et al., 2018), and action observation (e.g., Hardwick, Caspers, Eickhoff, & Swinnen, 2018; Molenberghs, Cunningham, & Mattingley, 2011). In particular for the Theory of Mind and empathy, recent meta-analyses show limited convergence of brain activity across different task-types (e.g., Schurz et al., 2014; Timmers et al., 2018).

High task-related heterogeneity in brain activation for social cognition tasks may be driven by different factors. Part of this heterogeneity could reflect low-level stimulus and instruction-related processes, which might be less interesting for understanding social cognition (see e.g., Mar, 2011; Schurz et al., 2014). On the other hand, component processes of social cognition could be co-recruited in some tasks, and thus be flexibly combined across domains (topics). To illustrate, we observed that a subset of Theory of Mind tasks engage left inferior frontal areas (Schurz et al., 2014), which overlap with areas typically found in empathy and action observation studies. Likewise, several authors have hypothesized that Theory of Mind and empathy processes are engaged concurrently in some tasks, which they linked to concepts like “Cognitive Empathy” (e.g., Hooker, Verosky, Germine, Knight, & D'Esposito, 2010; Preston & de Waal, 2002; Shamay-Tsoory, Aharon-Peretz, & Perry, 2009) and “Affective Theory of Mind” (e.g., Mier et al., 2010a,b; Sebastian et al., 2012; Shamay-Tsoory & Aharon-Peretz, 2007). Similarly, researchers have proposed that action observation and empathy share common processes (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Gazzola, Aziz-Zadeh, & Keysers, 2006). Another type of social

cognition task, asking participants to inhibit the imitation of an observed action (see Darda & Ramsey, 2019 for a meta-analysis), has been thought to engage processes linked to both action observation and Theory of Mind (e.g., Brass, Ruby, & Spengler, 2009). As discussed by Happé, Cook, and Bird (2017), processes engaged by different social cognition tasks could be related in various forms. Tasks could broadly overlap in terms of engaged processes, or engage some common and some distinct processes. Alternatively, processes engaged by one task could be a sub-set of those engaged by others.

Taken together, these points suggest that multiple and functionally distinct component processes are combined by some Theory of Mind, empathy, and action observation tasks. The present review aims at delineating these functional processes in terms of resting-state networks, which offer a task-free demarcation of major networks of the brain and are assumed to indicate different types of functional processing (Cole, Ito, Bassett, & Schultz, 2016; Smith et al., 2009; Tavor et al., 2016). This approach enables us to delineate different types of processes implicated in social cognition tasks, without the need of referring to the supposed outlines of “Theory of Mind”, “empathy”, and “action observation” areas/networks. As the connectivity pattern of an area determines the inputs it receives and outputs that it can send, it is considered as an important constraint of its function (see Passingham, Stephan, & Kötter, 2002). Resting-state (e.g., Tavor et al., 2016) and diffusion-weighted (e.g., Osher et al., 2016; Saygin et al., 2016) imaging studies showed that (task-unrelated) connectivity patterns at individual voxels in the brain carry enough information to predict whether they will activate in certain experimental tasks. This predictive relationship has been found across a range of different cognitive tasks (see Tavor et al., 2016).

Our approach is also motivated by previous research suggesting overlap between areas of task activation and resting-state networks for each of the three topics we consider. Note, however, that resting-state networks cannot be linked to specific forms of social cognition in a one-to-one fashion. Rather, it has been argued that they reflect a history of co-activation between brain regions during cognitive activity, irrespective of cognitive domain (see e.g., Fair et al., 2007; Wig, Schlaggar, & Petersen, 2011). Researchers have proposed that social functions, in turn, are embedded into those resting-state networks that support a set of cognitively related or compatible processes (see e.g., Kanske, Böckler, Trautwein, & Singer, 2015). To illustrate, Theory of Mind tasks activate on average most frequently around bilateral temporo-parietal and anterior temporal cortex, medial prefrontal cortex, posterior cingulate, and precuneus (e.g., Amodio & Frith, 2006; Frith & Frith, 2006; Mitchell, 2009). These areas largely overlap with the so-called Default Mode Network (DMN), which is assumed to mediate self-generated cognition decoupled from the physical world (e.g., Andrews-Hanna, Smallwood, & Spreng, 2014). This function is compatible with processes engaged during some Theory of Mind tasks, where we do not have immediate perceptual access to others' mental states (see Buckner & Carroll, 2007; Bzdok et al., 2013; Frith & Frith, 2003; Lieberman, 2007; Mars et al., 2012a). Also for empathy and action observation, overlaps between areas of task activation and resting-state networks have been noticed. Brain

activity for empathy tasks falls typically in bilateral insular cortices, inferior frontal gyri, midcingulate cortex, supra-marginal gyri, and somatosensory cortices (e.g., Bzdok et al., 2012; Decety & Jackson, 2004; Kanske et al., 2015). Moreover, as empathy produces an emotional response in the observer, it also engages brain areas for emotion regulation (e.g., Kanske, Heissler, Schönfelder, Bongers, & Wessa, 2011; Steinbeis, Bernhardt, & Singer, 2015), such as the dorsolateral prefrontal cortex. These areas overlap with two resting-state networks, the Ventral Attention Network (VAN) and the Frontoparietal Network (FPN). In addition to functional activation, structural variations in these two networks are linked to empathy and Theory of Mind capacities as well (Valk et al., 2017). Studies on action observation typically found activation in bilateral fusiform, posterior temporal, parietal and premotor/inferior frontal areas (e.g., Caspers, Zilles, Laird, & Eickhoff, 2010; Hardwick et al., 2018; Molenberghs, Cunnington, & Mattingley, 2009; Van Overwalle & Baetens, 2009), which overlap with parts of yet another resting-state network, the Dorsal Attention Network (DAN). In the present review, we follow up on these previous observations by a systematic and quantitative assessment of overlaps.

While the first part of our review is assessing whether multiple distinct networks are engaged by individual social cognition tasks, we next review how these networks interact. Therefore, the second part of our review gives an overview of task-based connectivity studies on social cognition that analyzed cross-network interactions. In particular, we seek to characterize which networks tends to drive interactions, i.e., are “orchestrating” information exchange. We thus focus our review on studies of effective connectivity, which give results on direction and sign of interactions. In other words, we review how networks implicated in social cognition are influencing each other’s activity, and if interactions are positive (i.e., excitatory) or negative (i.e., inhibitory).

2. First part: characterizing network co-activations by comparing meta-analyses to resting-state networks

2.1. Methods

We carried out conjunction analyses to calculate overlaps between meta-analysis and resting-state connectivity maps.² For resting-state maps, we used the MNI-space version (“liberal mask”) of the seven network parcellation by Yeo et al. (2011). Meta-analysis maps were also given in MNI space. For one meta-analysis (Schurz et al., 2014), we re-analyzed data with a more recent software version (AES-SDM 4.31, Radua et al., 2012; www.sdmproject.com). This was done to obtain result maps in MNI space (while Schurz et al., 2014 originally reported results in Talairach space). To adjust images in terms

² Meta-analysis maps report areas which are consistently activated for a certain task type. For simplicity and brevity, we refer to these maps as “task-activation maps”. However, technically, most meta-analytic maps covered in this review indicate the strength of convergence across studies, rather than the strength of underlying brain activation.

of size and resolution, we ran a simple SPM reslice job for all meta-analysis maps, using Yeo et al.’s (2011) maps as image defining space. This was carried out with SPM12 (www.fil.ion.ucl.ac.uk/spm). Finally, as the Yeo et al. (2011) parcellation covers only cortical but no sub-cortical areas, we restricted (masked) all meta-analysis maps to these cortical areas for the calculation of overlaps.

For quantifying overlaps, we used a variant of the dice score: For each meta-analysis map, we determined the percentage of voxels falling within each different intrinsic connectivity network of the Yeo et al. (2011) parcellation. Therefore, with $i1$ being a meta-analysis map and $i2$ an intrinsic connectivity network, we calculated $(n \text{ voxels in } i1 \& i2) / (n \text{ voxels in } i1)$. By calculating percentages scaled to the total number of voxels comprising each meta-analysis, we aimed at using a comparable metric despite meta-analyses being different in overall size and voxel extent (as they were carried out using different methods and statistical thresholding). For all meta-analyses in our review, we show maps at the same thresholds as used in the original studies. Bar charts in Figs. 1–3 summarize the percentage scores.

For display purposes, we projected meta-analysis maps as well as outlines of the Yeo et al. (2011) seven network parcellation to a cortical surface. All maps were projected to the Human Connectome Project (HCP) group average template “HCP_S1200_inflated_MSMA11”, using the volume-to-surface function in `wb_command` (www.humanconnectome.org). Note that, for the sake of coherence among surfaces, we also projected an MNI-space version of Yeo et al.’s (2011) parcellation (“liberal mask”, https://surfer.nmr.mgh.harvard.edu/fswiki/CorticalParcellation_Yeo2011) to the HCP surface using the volume-to-surface function. While surfaces are presented for illustrative purposes, we refer to the bar charts in Figs. 1–3 for quantitative assessments of overlap (which are based on calculations in MNI volume space).

2.2. Tasks in our review

2.2.1. Theory of Mind

For Theory of Mind (see Fig. 1), we cover meta-analyses of a pooled sample and four individual task groups from Schurz et al. (2014). Among the task groups, False Belief tasks presented verbal stories about characters holding mistaken beliefs. Trait Judgment tasks presented personality trait words and asked participants to judge if they applied to a certain person (e.g., a celebrity). Both tasks groups show predominant activation in medial prefrontal cortex, precuneus, and bilateral temporo-parietal cortex—areas which have been frequently mentioned in reviews of Theory of Mind task-activation (e.g., Frith & Frith, 2003; Koster-Hale & Saxe, 2013; Mitchell, 2009; Murray, Schaer, & Debbane, 2012; Van Overwalle, 2009).

Furthermore, we included two task groups from the same meta-analysis for which we also found activation in fronto-temporal areas—Social Animations and Reading the Mind in the Eyes tasks. Tasks from the former group showed animations of simple geometric shapes moving in a way which resembled intentional or social interactions. Tasks from the latter group presented photographs of eye-regions of faces and asked participants which mental-state word best

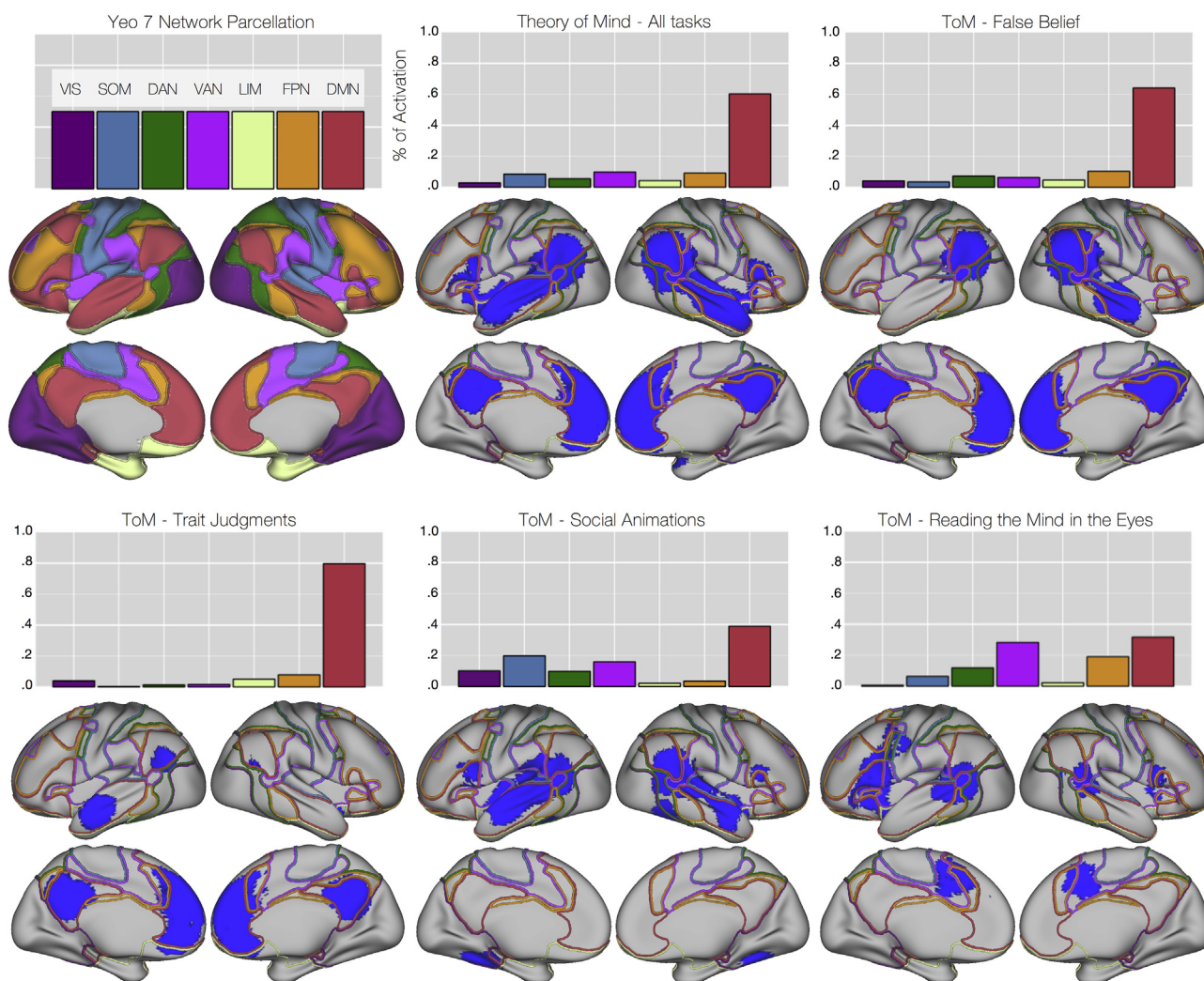


Fig. 1 – Meta-analysis maps displayed on the cortical surface, along with the borders of the Yeo 7 Network parcellation (Yeo et al., 2011). We show meta-analysis maps for a pooled Theory of Mind sample (All tasks), and task groups False Belief, Trait Judgments, Social Animations, and Reading the Mind in the Eyes (Schurz et al., 2014). Bar charts show the percentage of voxels from each meta-analysis map which fall into different intrinsic connectivity networks. Networks: VIS, Visual Network; SOM, Somatomotor Network; DAN, Dorsal Attention Network; VAN, Ventral Attention Network; LIM, Limbic Network; FPN, Frontoparietal Network; DMN, Default Mode Network.

described the state of the persons depicted. Based on observing activation in inferior frontal areas for both tasks, we have suggested (Schurz et al., 2014) that the Theory of Mind network receives support from areas linked to action observation and mirroring in these contexts. Moreover, performance on the Reading the Mind in the Eyes task was found to be related more strongly to individual differences in alexithymia than autism spectrum disorder (Oakley, Brewer, Bird, & Catmur, 2016), which suggests that it measures emotion recognition ability, in addition to (or even rather than) ToM abilities. Besides the four Theory of Mind task groups shown in Fig. 1, we show overlaps for further task groups³ from the

³ These additional two meta-analyses show highly similar patterns of overlap as found for False Belief and Trait Judgment tasks, which is why we do not present them in the main text for sake of brevity.

meta-analysis by Schurz et al. (2014) in Supplementary Figure 1.

2.2.2. Empathy

In Fig. 2, we show a pooled meta-analysis of empathy and four maps from different empathy task categories (Timmers et al., 2018). The authors split the empathy meta-analysis according to two orthogonal factors. First, the sample was divided into Cognitive/Evaluative tasks (e.g., ratings of pain or emotional states in other persons) versus Perceptual/Affective tasks (i.e., no task instructions, passive observation of others' emotional states). Second, it was distinguished between Pain tasks (i.e., presenting pain stimuli, such as displays of painful stimulation or painful facial expressions) and Non-Pain Negative Affect tasks (e.g., presenting displays of facial expressions or emotional scenes). Among these subgroups, we expect in particular Cognitive/Evaluative Empathy tasks to activate

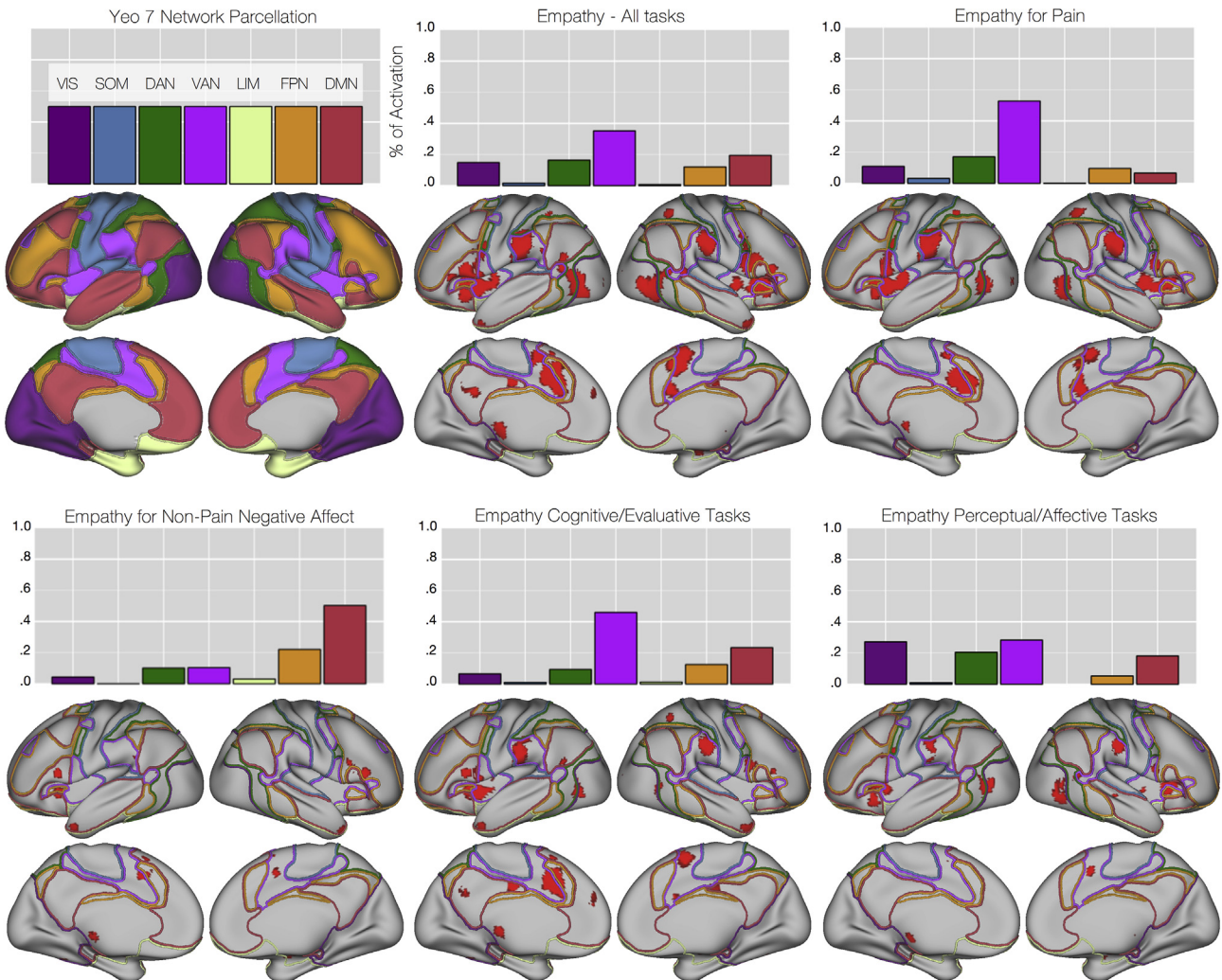


Fig. 2 – Meta-analysis maps displayed on the cortical surface, along with the borders of the Yeo 7 Network parcellation (Yeo et al., 2011). For empathy, maps from the meta-analysis by Timmers et al. (2018) are shown separately for a pooled meta-analysis (All tasks), and the task categories Pain, Non-Pain Negative Affect, Cognitive/Evaluative, and Perceptual/Affective. Bar charts show the percentage of voxels from each meta-analysis map which fall into different intrinsic connectivity networks. Networks: VIS, Visual Network; SOM, Somatomotor Network; DAN, Dorsal Attention Network; VAN, Ventral Attention Network; LIM, Limbic Network; FPN, Frontoparietal Network; DMN, Default Mode Network.

Theory of Mind and affect-processing areas conjointly. Several researchers have linked more cognitive forms of empathy to Theory of Mind processes (e.g., Dziobek et al., 2011; Hooker, Verosky, Germine, Knight, & D’Esposito, 2010; Shamay-Tsoory et al., 2009). Besides the contrasts shown in Fig. 2, additional contrasts carried out by Timmers et al. (2018) are shown in Supplementary Figure 1.

2.2.3. Action observation

For action observation (see Fig. 3), we included the meta-analyses of a pooled sample and three individual task groups—Arm, Leg, and Face Movement Observation tasks (Hardwick et al., 2018). All task groups contained passive paradigms, in which participants were asked to merely observe presented movement. Whereas Arm and Leg Movement Observation tasks tapped more strongly into processing of purely motor-related information, part of the

Face Movement Observation tasks also contained emotional content conveyed by facial expressions. This links the latter task group to empathy; also in the empathy meta-analyses included in our review, a fraction of tasks presented painful or emotional facial expressions.

2.3. Findings

As shown in Figs. 1–3, only a small number of task activation maps showed clear preference for a single intrinsic connectivity network in terms of overlap. The most noticeable examples for this pattern were found in the Theory of Mind field, namely False Belief and Trait Judgment tasks. To illustrate, around 80% of brain regions engaged for Trait Judgments fell within the Default Mode Network. All the other network-overlaps comprised less than 10% of that task activation map. For the topics empathy and action observation, task

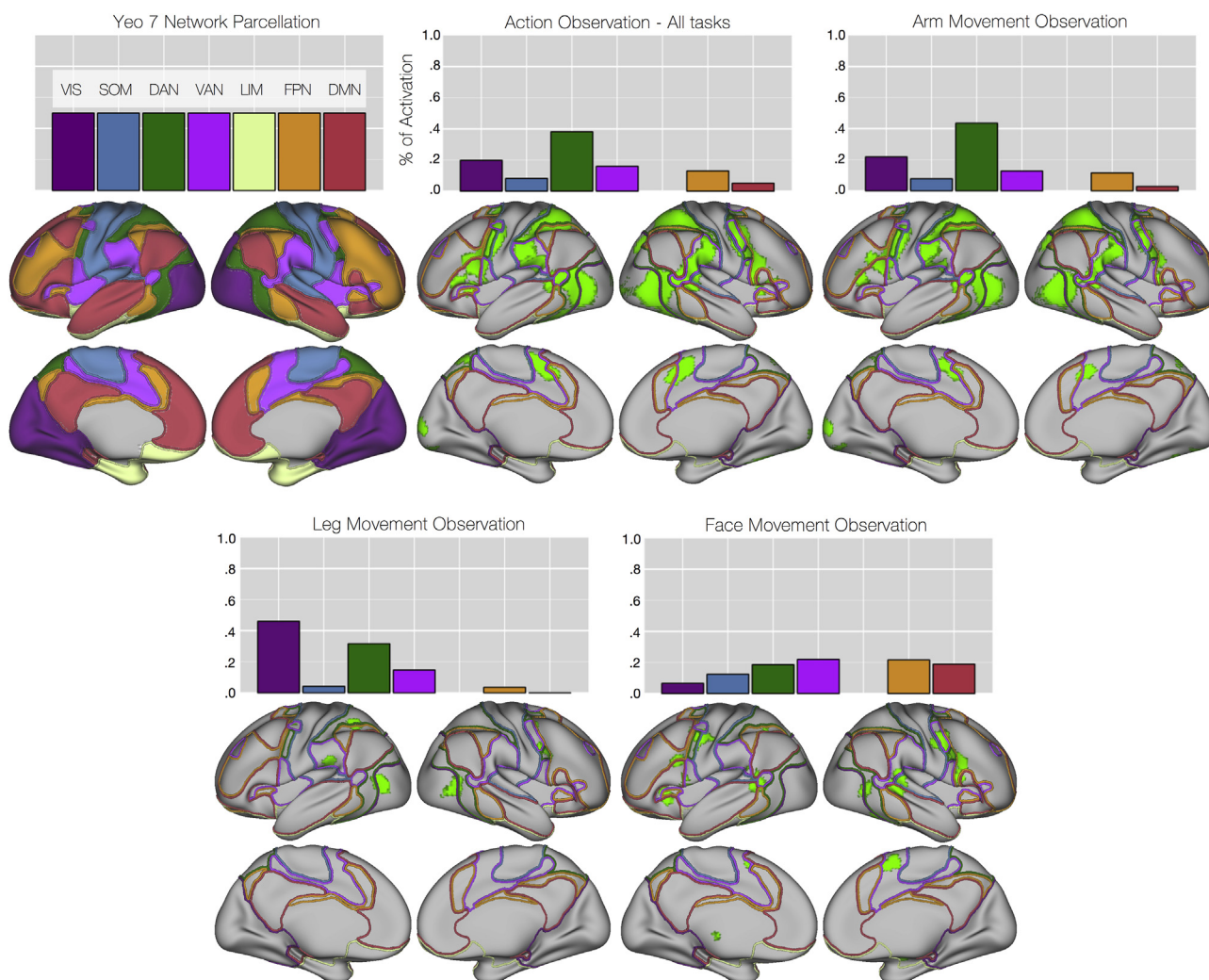


Fig. 3 – Meta-analysis maps displayed on the cortical surface, along with the borders of the Yeo 7 Network parcellation (Yeo et al., 2011). For action observation, we show meta-analysis maps for a pooled sample (All tasks), as well as Arm, Leg, and Face Movement Observation tasks individually (Hardwick et al., 2018). Bar charts show the percentage of voxels from each meta-analysis map which fall into different intrinsic connectivity networks. Networks: VIS, Visual Network; SOM, Somatomotor Network; DAN, Dorsal Attention Network; VAN, Ventral Attention Network; LIM, Limbic Network; FPN, Frontoparietal Network; DMN, Default Mode Network.

groups showed less strong preferences in overlap. Highest overlaps were found for the tasks Empathy for Pain (Ventral Attention Network) and Observing Arm Movement (Dorsal Attention Network), respectively. However, in both cases, networks of highest overlap only contained about half of task-active areas (53% and 43%, respectively).

More distributed patterns were found for a number of tasks for each of the three topics. Among these, some tasks showed slightly preferential overlap with one network, but a comparable amount of overlap with the two next best overlapping networks. For example, for Social Animations (Theory of Mind), 39% of task-activation overlapped with the Default Mode Network, and 36% overlapped with the Ventral Attention and the Somatomotor Networks taken together. Similar patterns of overlap across three networks were found for the pooled meta-analyses (across all tasks) for empathy and action observation, as well as the task Observing Leg Movement. Moreover, a number of tasks showed even more broadly

distributed network overlap. Here, the highest amounts of overlap were not only found in a single, but at least in two different networks. This was the case, for example, for the Reading the Mind in the Eyes task from the Theory of Mind field (32% Default Mode and 28% Ventral Attention Network). Similar patterns were found for Perceptual Empathy and Face Movement Observation tasks.

3. Second part: effective connectivity findings on cross-network interactions

To follow up on our observations of joint engagement of multiple socially-relevant connectivity networks, we carried out a literature review on connectivity studies. We focused on studies reporting effective (i.e., directed) connectivity findings between areas from different socially-relevant networks. All studies we cover in this review relied on Dynamic Causal

Modeling (DCM, Friston, Harrison, & Penny, 2003) to estimate effective connectivity.

3.1. Methods

To identify studies reporting cross-network connectivity in the context of social tasks, we conducted a systematic literature search using PubMed and Web of Science databases in June and July of 2019. We conducted the following key word searches: First ('empathy' AND/OR 'Theory of Mind') AND ('dcm' OR 'granger causality modeling'), yielding 12 and 14 search items. In addition ('empathy' AND/OR 'Theory of Mind') AND ('effective connectivity'), yielding 335 and 52 search items. Due to our focused research question, we excluded a large part of retrieved studies (see exclusion criteria below). Further literature was found by forward and backward searches within reference lists of most recent and relevant studies found in our database search (yielding 14 additional items).

We limited our sample to studies applying methods of effective connectivity on fMRI data in healthy adult subjects, and presenting tasks which explicitly measured empathy (e.g., participants were asked to empathize with a person in a video clip) or Theory of Mind (e.g., participants were asked to identify what a person in a video clip was thinking about). These selection criteria excluded, for example, studies in which participants were merely observing emotional expressions, or were asked to label facial affect (e.g., Arioli et al., 2018; Torrisi, Lieberman, Bookheimer, & Altshuler, 2013). We furthermore excluded studies that focused on empathy-related features of spoken language (i.e., affective prosody, see Ethofer et al., 2006).

Because of our specific interest in cross-network interactions, we additionally excluded studies analyzing connectivity only for areas of one canonical resting-state network linked to social cognition (i.e., all areas falling either within the Default Mode, Ventral Attention, Frontoparietal, or Dorsal Attention Network). Similarly, we excluded studies analyzing connectivity only for one resting-state network linked to social cognition, and only low-level areas besides (Hillebrandt, Friston, & Blakemore, 2014; Pehrs et al., 2017). As the resting-state parcellation by Yeo et al. (2011) does not cover subcortical areas, we also excluded connectivity analyses that centrally feature cortical–subcortical interactions (e.g., amygdala: Bruneau, Jacoby, & Saxe, 2015; hippocampus: Pehrs, Zaki, Taruffi, Kuchinke, & Koelsch, 2018; cerebellum: Van Overwalle, Van de Steen, & Mariën, 2019). Moreover, as we were interested in directed connectivity, we excluded studies applying Psycho-Physiological Interaction (PPI) analysis to assess connectivity, as this method does not provide information about the direction of an interaction (e.g., Lamm, Meltzoff, & Decety, 2010; Zaki, Ochsner, Hanelin, Wager, & Mackey, 2007).

Seven studies matched all our selection criteria. In the following, we will give a short overview of these studies and their findings. Note that if studies reported effective connectivity for multiple conditions and modulatory effects, we report only the effect best reflecting a change in (cognitive or affective) mental state related contents. For example, the study by Regenbogen, Habel, and Kellermann (2013) reported

one main effect of emotional information, three different additional effects of incongruence between emotional channels, and one effect of incomprehensible speech. For simplicity, we only illustrate connectivity patterns related to the main effect of emotional information in Fig. 4 but mention the other conditions alongside.

3.2. Findings

Fig. 4 illustrates modulatory effects on cross-network connectivity found for social conditions in our reviewed studies. We organize these results by networks driving the interactions. In terms of signals originating from the Default Mode Network (DMN), two studies found top-down influences by medial prefrontal areas onto areas of the Ventral Attention Network (VAN) and Dorsal Attention Network (DAN). In particular, a False Belief reasoning study (Schuwerk et al., 2014) reported negative coupling, that is, inhibitory influence,⁴ whereas a perspective taking study (Hillebrandt, Dumontheil, Blakemore, & Roiser, 2013) found positive coupling, that is, excitatory influence. In terms of signals driven by areas of the VAN, a social attentional reorienting task (Schuwerk, Schurz, Müller, Rupprecht, & Sommer, 2017) reported positive bottom-up signalling from a posterior medial temporal area (sometimes referred to as TPJ anterior, e.g., Bzdok et al., 2013; Mars et al., 2012b) to the anterior cingulate cortex in the DMN.

Finally, two patterns of interactions were found for the Frontoparietal Network (FPN). Two studies from the empathy field (Kanske, Böckler, Trautwein, Parianen Lesemann, & Singer, 2016; Regenbogen et al., 2013) found negative signalling from frontal (mPFC, insula) areas of the FPN,⁵ exerted onto temporo-parietal areas of the DMN. Both of these studies used tasks in which participants were asked to process feelings (and thoughts) of persons presented via video. By contrast, a study (Tettamanti et al., 2017) on mentalizing based on linguistic input (i.e., inferring the intention conveyed by a person's utterances or gestures) found left and right inferior frontal areas within the FPN to drive activation in DMN areas. Similarly, Van Ackeren, Smaragdi, and Rueschemeyer (2016) asked participants to infer speaker's intentions (indirect speech) and found an inferior frontal area to have a positive influence on DMN areas. Note, however, that in that study, the inferior frontal area was falling into the VAN rather than the FPN.

4. Discussion

In this review, we compared meta-analyses on three prominent topics in social cognition research—Theory of Mind,

⁴ Note that in a DCM analysis, positive coupling parameters indicate that an increase in area A is associated with an increase in area B, which we will refer to as excitatory (for simplicity). Negative coupling parameters indicate that an increase in area A is associated with a decrease in area B, and thus an inhibitory relationship.

⁵ Note that the medial prefrontal area in the DCM study by Regenbogen et al. (2013) was actually located at the border of the FPN and DMN.

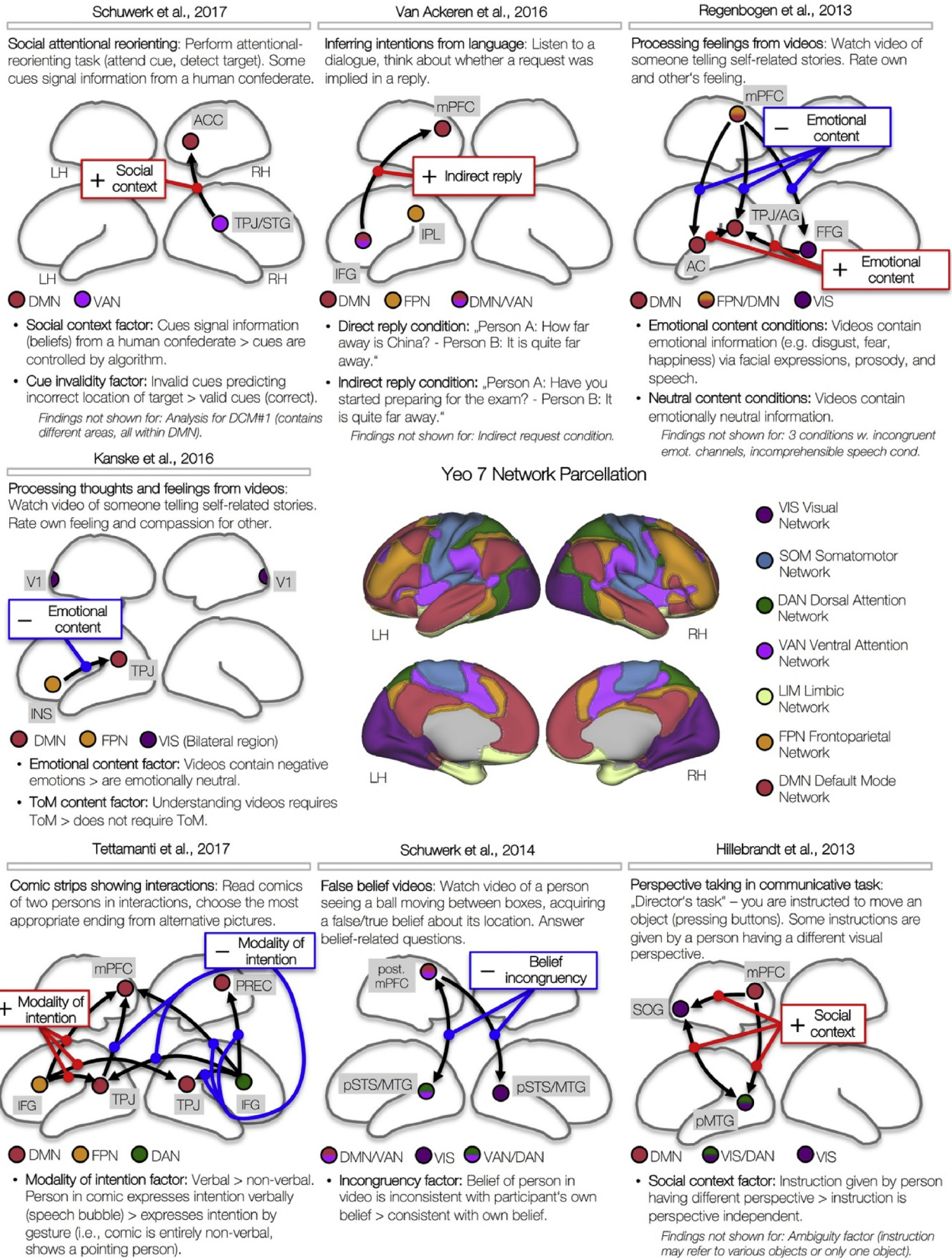


Fig. 4 – Cross-network connectivity in social tasks. Arrows indicate direction of signalling, red lines indicate positive (excitatory), blue lines negative (inhibitory) modulation of coupling. Abbreviations: INS, Insula; mPFC, medial Prefrontal Cortex; ACC, Anterior Cingulate Cortex; IFG, Inferior Frontal Gyrus; TPJ, Temporoparietal Junction; MTG, Middle Temporal Gyrus; STG/STS, Superior Temporal Gyrus/Sulcus; AG, Angular Gyrus; IPL, Inferior Parietal Lobule; SOG, Superior Occipital Gyrus; V1, Area V1; PREC, Precuneus; AC, Auditory Cortex; FFG, Fusiform Gyrus; p/post, posterior.

empathy, and action observation. We evaluated whether brain activation for different tasks probing these cognitive abilities engages only one or several more basic (resting-state) networks of the brain. In addition, we reviewed findings of effective connectivity studies to sort out how areas from different networks interact during social cognition tasks. Our main hypothesis was that a part of Theory of Mind, empathy, and action observation tasks co-recruit multiple functionally distinct processes and corresponding brain networks.

4.1. Co-activation of multiple networks implicated in social cognition

In the first part of our manuscript we reviewed the overlap between resting-state networks and areas of task activation found in meta-analyses of Theory of Mind, empathy, and action observation. Coherence among these two types of neuroimaging evidence varied considerably. For some tasks, in particular from the Theory of Mind field, activation maps showed strong correspondence with a single network (e.g., the Default Mode Network). For other cases, however, task activation was distributed across multiple different networks. For all three topics, we found tasks for which activation overlapped both with the Default Mode and the Ventral Attention Network. Among them were, for example, Reading the Mind in the Eyes tasks (Theory of Mind), Cognitive/Evaluative Empathy tasks, and Face Movement Observation tasks (action observation).

The fact that we found strong variability in correspondence between resting-state networks and meta-analytic maps also supports the soundness of our analysis approach. Meta-analytic maps are spatially smooth in nature. In principle, this could lead to generally diffuse overlap, that is, all task-activation networks falling into multiple distinct resting-state networks (because of high spatial smoothness of the former). We observed a different pattern of results. To illustrate, one Theory of Mind task (Trait Judgments) had an overlap of 80% with one network, compared to only 7% with the next best matching network. In contrast, for another Theory of Mind task (Reading the Mind in the Eyes), we found overlap values of 32% and 28% for this comparison. Both of these task-maps were created with the same meta-analysis method and identical smoothing (see Radua et al., 2012 for methods). This speaks against the concern that distributed patterns of overlap are only a consequence of strong meta-analytic smoothing. Note also that at least equally strong smoothing was applied for the meta-analyses we mentioned (Schurz et al., 2014), and the other meta-analyses covered in this review (Hardwick et al., 2018; Timmers et al., 2018; see Eickhoff et al., 2009 for methods).

4.2. Cross-network interactions

Given the co-activations of different networks we have reviewed, an outstanding question is whether and how these networks interact with each other. In the second part of our review, we summarized effective connectivity studies analyzing cross-network interactions. We organize our discussion of these findings along a prominent theme in network neuroscience—interactions between the Default Mode and

“Control Networks” (e.g., Cole, Repovš, & Anticevic, 2014; Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008). The latter term subsumes three important networks for this review, the Ventral Attention, Dorsal Attention, and the Frontoparietal Network.

4.2.1. Negative coupling (segregation) between Default Mode and Control Networks

A well-documented finding of cross-network interaction is the inhibitory and competitive relationship between the Default Mode Network and Control Networks. The Default Mode Network has been found to decrease its activity during tasks that require externally focused attention (e.g., Mazoyer et al., 2001; Raichle et al., 2001; Shulman et al., 1997). Moreover, studies found an inhibitory relationship between the Ventral Attention and the Default Mode Network, which has been considered to reflect the former down-regulating the latter to reduce interference from task-unrelated processes (Goulden et al., 2014; Wen, Liu, Yao, & Ding, 2013; Trautwein, Singer, & Kanske, 2016; see also Anticevic et al., 2012). At passive rest, Default Mode and Ventral Attention Networks have been found unrelated (e.g., Alcalá-López et al., 2018) and sometimes anti-correlated in terms of activity (Bzdok et al., 2013; Chai, Castañón, Öngür, & Whitfield-Gabrieli, 2012; Fox et al., 2005; Zhou et al., 2018). In a task-based fMRI study, Trautwein et al. (2016) analyzed functional connectivity for a combined stimulus-driven reorienting and executive control paradigm. The authors could show that both attentional control processes, which are linked to distinct control networks in the brain, have a similar down-regulating effect on the Default Mode Network.

Consistent with these findings of inhibitory interactions, our review of effective connectivity studies found negative signalling from the Frontoparietal to the Default Mode Network. Two studies presenting affective contents (Kanske et al., 2016; Regenbogen et al., 2013) found a negative signal from frontal (mPFC, insula) areas of the Frontoparietal Network, exerted onto temporo-parietal areas of the Default Mode Network. A commonality of these studies is that they presented videos of persons telling emotional autobiographical stories. Kanske et al. (2016) suggested that the negative coupling could reflect that affective processes (i.e., empathizing) are taking precedence relative to mentalizing. Autobiographical stories are rich and naturalistic stimuli, which provide grounds for both empathizing and mentalizing. Therefore, inhibition of Default Mode Network activation could reflect focusing of attention on those aspects of the social input that potentially require the most immediate action (see Menon & Uddin, 2010).

Besides, we found another pattern of negative coupling in a belief-reasoning study by Schuwerk et al. (2014). Participants viewed a false-belief cartoon animation (about object location) and were asked to make own-belief and other-belief judgments. For this task, the authors found a negative top-down signal from the medial prefrontal cortex (Default Mode Network) to posterior temporal areas (at the border between Ventral/Dorsal Attention Networks). Although the literature has reported inhibitory influences in this direction less frequently, some theoretical accounts are in line with such a pattern. Researchers have hypothesized that posterior parts of

medial prefrontal cortex implement a “decoupling” process for Theory of Mind (e.g., Gallagher & Frith, 2003; Frith & Frith, 2003; see also; Leslie, Friedman, & German, 2004; Rothmayer et al., 2011; Döhnel et al., 2012; Sommer et al., 2007). This process is thought to separate belief representations from representations of reality. Based on this idea, inhibitory signals from the posterior medial prefrontal cortex (i.e., the Default Mode Network) may down-regulate bottom-up signals from the Ventral Attention Network, which convey new information about ongoing external events. For example, for maintaining a representation of another person's belief, novel incoming information about how reality changes needs to be separated.

Consistent with the notion of segregation, behavioral and patient studies also found some Theory of Mind (i.e., Default Mode) and empathy (i.e., Ventral Attention) related processes to be largely independent (Reiter, Kanske, Eppinger, & Li, 2017; Stietz, Jauk, Krach, & Kanske, 2019; Winter, Spengler, Bermpohl, Singer, & Kanske, 2017). In the “EmpaToM” task, Kanske et al. (2016) used a combined task framework that behaviourally measured Theory of Mind (accuracy and speed in inferring other's beliefs) and empathy (emotional valence ratings) in a large group of healthy adults (see also Kanske et al., 2015). The two measures were uncorrelated. In a further analysis that combined Theory of Mind and empathy measures from additional tasks, the authors found no correlation either. Also, studies that tested more cognitive (Strange Stories) versus more affective (Reading the Mind in the Eyes) measures of Theory of Mind found no correlation between them (Dziobek et al., 2006; Rice, Moraczewski, & Redcay, 2016). Furthermore, studies in brain damaged patients found a double-dissociation between cognitive and affective forms of Theory of Mind (Shamay-Tsoory & Aharon-Peretz, 2007; see also Shamay-Tsoory et al., 2009).

4.2.2. Positive coupling (integration) between Default Mode and Control Networks

Functional networks and their interactions are constrained by underlying structural brain connectivity (e.g., Bullmore & Sporns, 2009; Honey et al., 2009). Therefore, classic findings of segregation between Default Mode and Control Networks presumably reflect a predominant pattern of network interaction over time. Nevertheless, recent studies have pointed out another pattern of cross-network interaction, which takes place during particular cognitive states. For cognitively demanding tasks, large scale networks of the brain have shown to increase their integration (i.e., form positive associations). A prominent example are increases in global network integration for higher-levels of N-back working memory tasks (e.g., Shine et al., 2016; Vatansever, Menon, Manktelow, Sahakian, & Stamatakis, 2015; Wendelken, Ferrer, Whitaker, & Bunge, 2016). Shine et al. (2016) could further show that network integration increases across a variety of other cognitive tasks (compared to passive rest). In that study, a Theory of Mind task (Social Animations) and an N-Back working memory task showed the highest integration. Researchers hypothesized that high network integration reflects a response to task complexity, characterized by goal-directedness and cognitive control (for a review, see Shine & Poldrack, 2018).

Concerning network integration, it is interesting to note that the Default Mode Network mainly consists of richly connected network “hubs” (Barbey et al., 2018; Gu et al., 2015). For example, the precuneus and posterior cingulate cortex are thought to build a structural “core” of the brain, and to have the highest number of connections with other areas/networks of the brain (Hagmann et al., 2008; Van den Heuvel & Sporns, 2013). Based on a comprehensive analysis of brain structure, functional connectivity, and large-scale meta-analytic activation, Margulies et al. (2016) argued that the far-reaching pattern of connectivity of the Default Mode Network enables to establish highly multimodal and abstract representations. Somewhat relatedly, the “global workspace” model posits that the Default Mode Network provides a hub for generating highly associative representations (e.g., Dehaene & Changeux, 2011; Vatansever et al., 2015).

In this light, several positive cross-network interactions identified in our review are of interest. Tettamanti et al. (2017) as well as Van Ackeren et al. (2016) asked participants to infer others' mental states based on linguistic information (i.e., inferring intentions conveyed by a person's utterances). Both studies found that the left inferior frontal gyrus (as part of Frontoparietal Network/Ventral Attention Networks) drives activation in areas of the Default Mode Network. This pattern is compatible with the idea that areas of the Default Mode Network integrate information for generating abstract representations: Language processing areas parse linguistic input and then forward that information to the Default Mode Network for subsequent analysis (e.g., mentalizing). Notably, Tettamanti et al., 2017 additionally reported negative signaling from the right inferior frontal gyrus (Dorsal Attention Network) to multiple Default Mode Network areas. This pattern was found for a second experimental condition, in which participants were asked to infer intentions from gestures, rather than speech. However, due to the way the DCM analysis was set up in that study (i.e., specification of regressors), these negative coupling values indicated reduced coupling for speech versus gesture conditions. In other words, coupling was relatively stronger (less negative) during the gesture condition. Based on the notion of the Default Mode Network as an information integrator, we speculate that this could reflect that right inferior frontal areas are implicated in parsing non-verbal gestural information, and then send the results to Default Mode areas for further analysis. Several functional connectivity studies based on Psycho-Physiological Interaction (PPI) analysis support a similar interpretation. In various settings, participants were asked to infer others' intentions or beliefs from their actions. The main result of those studies was that connectivity between Default Mode Network (medial prefrontal and temporo-parietal cortex) and fronto-parietal action observation areas was increased (Ciaramidaro, Becchio, Colle, Bara, & Walter, 2014; Sperduti, Guionnet, Fossati, & Nadel, 2014; Spunt & Lieberman, 2012a,b; Thioux, Suttrup, & Keysers, 2018; see also Schippers, Gazzola, Goebel, & Keysers, 2009; Schippers, Roebroek, Renken, Nanetti, & Keysers, 2010).

Besides studies that found influence from inferior frontal areas on the Default Mode Network, our review also contained one study (Schuwerk et al., 2017) which found bottom-up signalling from the posterior middle temporal gyrus (Ventral

Attention Network) to the anterior cingulate cortex (Default Mode Network). Here, participants performed an attention-reorienting task in a social context, i.e., they were told that attention cues signal another person's expectation (belief) about where the target will appear. Again, this finding is compatible with the idea that the Default Mode Network integrates information from other networks. Specifically, posterior temporal areas may be involved in processing information about a social context and forward the output to the Default Mode Network for further processing. Another study in our review, however, shows a less coherent result pattern. Hillebrandt et al. (2013) found a positive top-down signal from a Default Mode Network area (anterior cingulate cortex) to posterior temporal and visual areas that are part of the Dorsal Attention and Visual Networks. This finding goes in the opposite direction compared to previous ones, suggesting that the Default Mode Network is the source of signals, rather than receiving them. Hillebrandt et al. (2013) suggested that their results could reflect Default Mode Network areas inhibiting low-level visual representations by regulating activation in the area. While such an interpretation is consistent with negative coupling as discussed in the preceding section (rather than global integration), further evidence is necessary to disambiguate findings.

4.3. Summary and outlook

We have reviewed how task-activation for social cognition studies maps onto basic connectivity networks of the brain. Correspondence was found at varying degrees. For some tasks, we found high overlap with a single connectivity network. For other tasks, widely distributed patterns of overlap were found, which indicates that they engage functionally distinct networks in parallel. To characterize how areas from these different networks interact with another, we reviewed effective connectivity studies on social cognition. Findings show two types of cross-network interactions: Negative coupling (i.e., segregation) and positive coupling (integration) between different networks. Finding both segregation and integration among networks does not imply a contradiction, but rather reflects two rivaling constraints on cognitive function (e.g., Shine & Poldrack, 2018). While segregation enables functional specialization, integration enables neural flexibility. In terms of cognitive processing, it has been hypothesized that network integration reflects more controlled and effortful processing (e.g., Kitzbichler, Henson, Smith, Nathan, & Bullmore, 2011; Shine & Poldrack, 2018; Vatansever et al., 2015). This relationship could help to characterize social cognitive tasks. Researchers have hypothesized that one fundamental difference among cognitive components of social cognition (e.g., Apperly & Butterfill, 2009; Happé et al., 2017) is whether they are efficient and automatic versus effortful and controlled. Interestingly, however, several neuroimaging studies reported common areas activated for automatic versus controlled tasks. For example, researchers observed that “implicit” (i.e. simple, uninstructed and requiring little control) and “explicit” Theory of Mind tasks recruit overlapping brain areas (e.g., Bardi, Desmet, Nijhof, Wiersema, & Brass, 2016; Bardi, Six, & Brass, 2017; Boccadoro et al., 2019; Naughtin et al., 2017; Nijhof, Bardi, Brass, & Wiersema, 2018; see also; Van Overwalle &

Vandekerckhove, 2013). Looking at patterns of network integration in such studies could further specify how the same brain areas may implement more effortful versus more automatic mentalizing via different patterns of network interactions.

Finally, the reviewed evidence on cross-network integration may highlight mechanisms relevant for more naturalistic (and complex) forms of social cognition. Studies presenting more vivid social stimuli, such as scenes or videos of social interactions (e.g., Deuse et al., 2016; Wolf, Dziobek, & Heekeren, 2010), found areas linked to Theory of Mind and empathy to be jointly activated. Moreover, co-activation of areas linked to Theory of Mind and action observation has been found during interpersonal interactions (see Schilbach et al., 2013), which undoubtedly play a central role in everyday social life. For example, in an fMRI study, Schilbach, Eickhoff, Mojzisch, and Vogeley (2008) measured social interactions in terms of brain activity related to facial mimicry. Results showed brain activation in the precuneus and other medial areas on the one hand, and premotor areas such as the precentral gyrus on the other hand. In another seminal study, Zaki, Weber, Bolger, and Ochsner (2009) asked participants to watch videos of people who were telling stories about autobiographical events. Participants were also asked to judge how the person in the video felt. Besides, the narrators in the video themselves reported their mood during story-telling. Participants were considered accurate in their empathic judgment if their judgment was close to the narrator's self-report. During moment of high accuracy, participants' brain activity was high both in areas linked to Theory of Mind (e.g., medial prefrontal cortex) and action observation (e.g., premotor cortex). Taken together, these studies once again highlight the idea that social abilities are not only characterized by activation levels of isolated networks, but also by the level of information integration between them.

Declaration of Competing Interest

No competing interests to declare.

None of the procedures or analyses used in this review have been pre-registered in a time-stamped, institutional registry.

Acknowledgements

For illustration of our Figures we used brain images (e.g. background reference images) created by the Human Connectome Project, WU-Minn Consortium (Principal Investigators: David Van Essen and Kamil Ugurbil; 1U54MH091657) funded by the 16 NIH Institutes and Centers that support the NIH Blueprint for Neuroscience Research; and by the McDonnell Center for Systems Neuroscience at Washington University. MS was financially supported by an Erwin Schrödinger Fellowship (FWF-J4009-B27) and a Marie Skłodowska-Curie Individual Fellowship (MSCA-IF 844734). The Wellcome Centre for Integrative Neuroimaging is supported by core funding from the Wellcome Trust (203139/Z/16/

Z). LM was supported by a scholarship of the Friedrich Ebert Foundation. PK was supported by the German Federal Ministry of Education and Research within the ASD-Net (BMBF FKZ 01EE1409A), the German Research Foundation (KA 4412/2-1) and Die Junge Akademie at the Berlin-Brandenburg Academy of Sciences and Humanities and the German National Academy of Sciences Leopoldina. MS and PK were additionally supported by the German Research Foundation Network 'Understanding Others' (SCHN 1481/2-1).

Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cortex.2020.05.006>.

REFERENCES

- Adolphs, R. (2009). The social brain: Neural basis of social knowledge. *Annual Review of Psychology*, 60(1), 693–716. <https://doi.org/10.1146/annurev.psych.60.110707.163514>.
- Alcalá-López, D., Smallwood, J., Jefferies, E., Van Overwalle, F., Vogeley, K., Mars, R. B., ... Bzdok, D. (2018). Computing the social brain connectome across systems and states. *Cerebral Cortex*, 28(7), 2207–2232. <https://doi.org/10.1093/cercor/bhx121>.
- Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: The medial frontal cortex and social cognition. *Nature Reviews Neuroscience*, 7(4), 268. <https://doi.org/10.1038/nrn1884>.
- Andrews-Hanna, J. R., Smallwood, J., & Spreng, R. N. (2014). The default network and self-generated thought: Component processes, dynamic control, and clinical relevance. *Annals of the New York Academy of Sciences*, 1316(1), 29–52. <https://doi.org/10.1111/nyas.12360>.
- Anticevic, A., Cole, M. W., Murray, J. D., Corlett, P. R., Wang, X.-J., ... Krystal, J. H. (2012). The role of default network deactivation in cognition and disease. *Trends in Cognitive Sciences*, 16(12), 584–592. <https://doi.org/10.1016/j.tics.2012.10.008>.
- Apperly, I. A., & Butterfill, S. A. (2009). Do humans have two systems to track beliefs and belief-like states? *Psychological Review*, 116(4), 953. <https://doi.org/10.1037/a0016923>.
- Arioli, M., Perani, D., Cappa, S., Proverbio, A. M., Zani, A., Falini, A., ... Canessa, N. (2018). Affective and cooperative social interactions modulate effective connectivity within and between the mirror and mentalizing systems. *Human Brain Mapping*, 39(3), 1412–1427. <https://doi.org/10.1002/hbm.23930>.
- Barbey, A. K. (2018). Network neuroscience theory of human intelligence. *Trends in Cognitive Sciences*, 22(1), 8–20. <https://doi.org/10.1016/j.tics.2017.10.001>.
- Bardi, L., Desmet, C., Nijhof, A., Wiersema, J. R., & Brass, M. (2016). Brain activation for spontaneous and explicit false belief tasks overlaps: New fMRI evidence on belief processing and violation of expectation. *Social Cognitive and Affective Neuroscience*, 12(3), 391–400. <https://doi.org/10.1093/scan/nsw143>.
- Bardi, L., Six, P., & Brass, M. (2017). Repetitive TMS of the temporoparietal junction disrupts participant's expectations in a spontaneous Theory of Mind task. *Social Cognitive and Affective Neuroscience*, 12(11), 1775–1782. <https://doi.org/10.1093/scan/nsx109>.
- Boccadoro, S., Cracco, E., Hudson, A. R., Bardi, L., Nijhof, A. D., Wiersema, J. R., ... Mueller, S. C. (2019). Defining the neural correlates of spontaneous Theory of Mind (ToM): An fMRI multi-study investigation. *NeuroImage*, 203, 1161–1193. <https://doi.org/10.1016/j.neuroimage.2019.116193>.
- Brass, M., Ruby, P., & Spengler, S. (2009). Inhibition of imitative behaviour and social cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1528), 2359–2367. <https://doi.org/10.1098/rstb.2009.0066>.
- Bruneau, E. G., Jacoby, N., & Saxe, R. (2015). Empathic control through coordinated interaction of amygdala, theory of mind and extended pain matrix brain regions. *NeuroImage*, 114, 105–119.
- Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., ... Rizzolatti, G. (2004). Neural circuits involved in the recognition of actions performed by nonconpecifics: An fMRI study. *Journal of Cognitive Neuroscience*, 16(1), 114–126. <https://doi.org/10.1162/089982904322755601>.
- Buckner, R. L., & Carroll, D. C. (2007). Self-projection and the brain. *Trends in Cognitive Sciences*, 11(2), 49–57. <https://doi.org/10.1016/j.tics.2006.11.004>.
- Bullmore, E., & Sporns, O. (2009). Complex brain networks: Graph theoretical analysis of structural and functional systems. *Nature Reviews Neuroscience*, 10(3), 186–198. <https://doi.org/10.1038/nrn2575>.
- Bzdok, D., Langner, R., Schilbach, L., Jakobs, O., Roski, C., Caspers, S., ... Eickhoff, S. B. (2013). Characterization of the temporo-parietal junction by combining data-driven parcellation, complementary connectivity analyses, and functional decoding. *NeuroImage*, 81, 381–392. <https://doi.org/10.1016/j.neuroimage.2013.05.046>.
- Bzdok, D., Schilbach, L., Vogeley, K., Schneider, K., Laird, A. R., Langner, R., ... Eickhoff, S. B. (2012). Parsing the neural correlates of moral cognition: ALE meta-analysis on morality, theory of mind, and empathy. *Brain Structure & Function*, 217(4), 783–796. <https://doi.org/10.1007/s00429-012-0380-y>.
- Carr, L., Iacoboni, M., Dubeau, M. C., Mazziotta, J. C., & Lenzi, G. L. (2003). Neural mechanisms of empathy in humans: A relay from neural systems for imitation to limbic areas. *Proceedings of the National Academy of Sciences*, 100(9), 5497–5502. <https://doi.org/10.1073/pnas.0935845100>.
- Caspers, S., Zilles, K., Laird, A. R., & Eickhoff, S. B. (2010). ALE meta-analysis of action observation and imitation in the human brain. *NeuroImage*, 50(3), 1148–1167. <https://doi.org/10.1016/j.neuroimage.2009.12.112>.
- Chai, X. J., Castañón, A. N., Öngür, D., & Whitfield-Gabrieli, S. (2012). Anticorrelations in resting state networks without global signal regression. *NeuroImage*, 59(2), 1420–1428. <https://doi.org/10.1016/j.neuroimage.2011.08.048>.
- Ciaramidaro, A., Becchio, C., Colle, L., Bara, B. G., & Walter, H. (2014). Do you mean me? Communicative intentions recruit the mirror and the mentalizing system. *Social Cognitive and Affective Neuroscience*, 9(7), 909–916. <https://doi.org/10.1093/scan/nst062>.
- Cole, M. W., Ito, T., Bassett, D. S., & Schultz, D. H. (2016). Activity flow over resting-state networks shapes cognitive task activations. *Nature Neuroscience*, 19(12), 1718. <https://doi.org/10.1038/nn.4406>.
- Cole, M. W., Repovš, G., & Anticevic, A. (2014). The frontoparietal control system: A central role in mental health. *The Neuroscientist*, 20(6), 652–664. <https://doi.org/10.1177/1073858414525995>.
- Darda, K. M., & Ramsey, R. (2019). The inhibition of automatic imitation: A meta-analysis and synthesis of fMRI studies. *NeuroImage*, 197, 320–329. <https://doi.org/10.1016/j.neuroimage.2019.04.059>.
- Decety, J., & Jackson, P. L. (2004). The functional architecture of human empathy. *Behavioral and Cognitive Neuroscience Reviews*, 3(2), 71–100. <https://doi.org/10.1177/1534582304267187>.

- Dehaene, S., & Changeux, J.-P. (2011). Experimental and theoretical approaches to conscious processing. *Neuron*, 70(2), 200–227. <https://doi.org/10.1016/j.neuron.2011.03.018>.
- Deuse, L., Rademacher, L. M., Winkler, L., Schultz, R. T., Gründer, G., & Lammertz, S. E. (2016). Neural correlates of naturalistic social cognition: Brain-behavior relationships in healthy adults. *Social Cognitive and Affective Neuroscience*, 11(11), 1741–1751. <https://doi.org/10.1093/scan/nsw094>.
- Döhl, K., Schuwerk, T., Meinhardt, J., Sodian, B., Hajak, G., & Sommer, M. (2012). Functional activity of the right temporoparietal junction and of the medial prefrontal cortex associated with true and false belief reasoning. *NeuroImage*, 60(3), 1652–1661. <https://doi.org/10.1016/j.neuroimage.2012.01.073>.
- Dosenbach, N. U., Fair, D. A., Cohen, A. L., Schlaggar, B. L., & Petersen, S. E. (2008). A dual-networks architecture of top-down control. *Trends in Cognitive Sciences*, 12(3), 99–105. <https://doi.org/10.1016/j.tics.2008.01.001>.
- Dziobek, I., Fleck, S., Kalbe, E., Rogers, K., Hassenstab, J., Brand, M., ... Convit, A. (2006). Introducing MASC: A movie for the assessment of social cognition. *Journal of Autism and Developmental Disorders*, 36(5), 623–636. <https://doi.org/10.1007/s10803-006-0107-0>.
- Dziobek, I., Preißler, S., Grodzanovic, Z., Heuser, I., Heekeren, H. R., & Roepke, S. (2011). Neuronal correlates of altered empathy and social cognition in borderline personality disorder. *NeuroImage*, 57(2), 539–548. <https://doi.org/10.1016/j.neuroimage.2011.05.005>.
- Eickhoff, S. B., Laird, A. R., Grefkes, C., Wang, L. E., Zilles, K., & Fox, P. T. (2009). Coordinate-based activation likelihood estimation meta-analysis of neuroimaging data: A random-effects approach based on empirical estimates of spatial uncertainty. *Human Brain Mapping*, 30(9), 2907–2926. <https://doi.org/10.1002/hbm.20718>.
- Ethofer, T., Anders, S., Erb, M., Herbert, C., Wiethoff, S., Kissler, J., ... Wildgruber, D. (2006). Cerebral pathways in processing of affective prosody: A dynamic causal modeling study. *NeuroImage*, 30(2), 580–587. <https://doi.org/10.1016/j.neuroimage.2005.09.059>.
- Fabrizio-Destro, M., & Rizzolatti, G. (2008). Mirror neurons and mirror systems in monkeys and humans. *Physiology*, 23(3), 171–179. <https://doi.org/10.1152/physiol.00004.2008>.
- Fair, D. A., Dosenbach, N. U., Church, J. A., Cohen, A. L., Brahmbhatt, S., Miezin, F. M., ... Schlaggar, B. L. (2007). Development of distinct control networks through segregation and integration. *Proceedings of the National Academy of Sciences*, 104(33), 13507–13512.
- Fan, Y., Duncan, N. W., de Greck, M., & Northoff, G. (2011). Is there a core neural network in empathy? An fMRI based quantitative meta-analysis. *Neuroscience and Biobehavioral Reviews*, 35(3), 903–911. <https://doi.org/10.1016/j.neubiorev.2010.10.009>.
- Fox, M. D., Snyder, A. Z., Vincent, J. L., Corbetta, M., Essen, D. C. V., & Raichle, M. E. (2005). The human brain is intrinsically organized into dynamic, anticorrelated functional networks. *Proceedings of the National Academy of Sciences*, 102(27), 9673–9678. <https://doi.org/10.1073/pnas.0504136102>.
- Friston, K. J., Harrison, L., & Penny, W. (2003). Dynamic causal modelling. *NeuroImage*, 19(4), 1273–1302. [https://doi.org/10.1016/s1053-8119\(03\)00202-7](https://doi.org/10.1016/s1053-8119(03)00202-7).
- Frith, U., & Frith, C. D. (2003). Development and neurophysiology of mentalizing. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 358(1431), 459–473. <https://doi.org/10.1098/rstb.2002.1218>.
- Frith, C. D., & Frith, U. (2006). The neural basis of mentalizing. *Neuron*, 50(4), 531–534. <https://doi.org/10.1016/j.neuron.2006.05.001>.
- Gallagher, H. L., & Frith, C. D. (2003). Functional imaging of 'theory of mind'. *Trends in Cognitive Sciences*, 7(2), 77–83. [https://doi.org/10.1016/S1364-6613\(02\)00025-6](https://doi.org/10.1016/S1364-6613(02)00025-6).
- Gallese, V. (2003). The roots of empathy: The shared manifold hypothesis and the neural basis of intersubjectivity. *Psychopathology*, 36(4), 171–180. <https://doi.org/10.1159/000072786>.
- Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences*, 2(12), 493–501. [https://doi.org/10.1016/S1364-6613\(98\)01262-5](https://doi.org/10.1016/S1364-6613(98)01262-5).
- Gazzola, V., Aziz-Zadeh, L., & Keysers, C. (2006). Empathy and the somatotopic auditory mirror system in humans. *Current Biology*, 16, 1824–1829. <https://doi.org/10.1016/j.cub.2006.07.072>.
- Goulden, N., Khusnulina, A., Davis, N. J., Bracewell, R. M., Bokde, A. L., McNulty, J. P., ... Mullins, P. G. (2014). The salience network is responsible for switching between the default mode network and the central executive network: Replication from DCM. *NeuroImage*, 99, 180–190. <https://doi.org/10.1016/j.neuroimage.2014.05.052>.
- Grafton, S. T., Arbib, M., Fadiga, L., & Rizzolatti, G. (1996). Localization of grasp representations in humans by positron emission tomography. 2. Observation compared with imagination. *Experimental Brain Research*, 112, 103–111. <https://doi.org/10.1007/BF00227183>.
- Gu, S., Pasqualetti, F., Cieslak, M., Telesford, Q. K., Yu, A. B., Kahn, A. E., ... Bassett, D. S. (2015). Controllability of structural brain networks. *Nature Communications*, 6, 8414. <https://doi.org/10.1038/ncomms9414>.
- Hagmann, P., Cammoun, L., Gigandet, X., Meuli, R., Honey, C. J., Wedeen, V. J., ... Sporns, O. (2008). Mapping the structural core of human cerebral cortex. *PLOS Biology*, 6(7), e159. <https://doi.org/10.1371/journal.pbio.0060159>.
- Happé, F., Cook, J. L., & Bird, G. (2017). The structure of social cognition: In (ter) dependence of sociocognitive processes. *Annual Review of Psychology*, 68, 243–267. <https://doi.org/10.1146/annurev-psych-010416-044046>.
- Hardwick, R. M., Caspers, S., Eickhoff, S. B., & Swinnen, S. P. (2018). Neural correlates of action: Comparing meta-analyses of imagery, observation, and execution. *Neuroscience and Biobehavioral Reviews*, 94, 31–44. <https://doi.org/10.1016/j.neubiorev.2018.08.003>.
- Hillebrandt, H., Dumontheil, I., Blakemore, S.-J., & Roiser, J. P. (2013). Dynamic causal modelling of effective connectivity during perspective taking in a communicative task. *NeuroImage*, 76, 116–124. <https://doi.org/10.1016/j.neuroimage.2013.02.072>.
- Hillebrandt, H., Friston, K. J., & Blakemore, S.-J. (2014). Effective connectivity during animacy perception—dynamic causal modelling of Human Connectome Project data. *Scientific Reports*, 4, 6240. <https://doi.org/10.1038/srep06240>.
- Honey, C. J., Sporns, O., Cammoun, L., Gigandet, X., Thiran, J. P., Meuli, R., ... Hagmann, P. (2009). Predicting human resting-state functional connectivity from structural connectivity. *Proceedings of the National Academy of Sciences of the United States of America*, 106(6), 2035–2040. <https://doi.org/10.1073/pnas.0811168106>.
- Hooker, C. I., Verosky, S. C., Germine, L. T., Knight, R. T., & D'Esposito, M. (2010). Neural activity during social signal perception correlates with self-reported empathy. *Brain Research*, 1308, 100–113. <https://doi.org/10.1016/j.brainres.2009.10.006>.
- Jackson, P. L., Meltzoff, A. N., & Decety, J. (2005). How do we perceive the pain of others? A window into the neural processes involved in empathy. *NeuroImage*, 24(3), 771–779. <https://doi.org/10.1016/j.neuroimage.2004.09.006>.
- Kanske, P. (2018). The social mind: Disentangling affective and cognitive routes to understanding others. *Interdisciplinary*

- Science Reviews, 43(2), 115–124. <https://doi.org/10.1080/03080188.2018.1453243>.
- Kanske, P., Böckler, A., Trautwein, F.-M., Parianen Lesemann, F. H., & Singer, T. (2016). Are strong empathizers better mentalizers? Evidence for independence and interaction between the routes of social cognition. *Social Cognitive and Affective Neuroscience*, 11(9), 1383–1392. <https://doi.org/10.1093/scan/nsw052>.
- Kanske, P., Böckler, A., Trautwein, F.-M., & Singer, T. (2015). Dissecting the social brain: Introducing the EmpaToM to reveal distinct neural networks and brain-behavior relations for empathy and Theory of Mind. *NeuroImage*, 122, 6–19. <https://doi.org/10.1016/j.neuroimage.2015.07.082>.
- Kanske, P., Heissler, J., Schönfelder, S., Bongers, A., & Wessa, M. (2011). How to regulate emotion? Neural networks for reappraisal and distraction. *Cerebral Cortex*, 21(6), 1379–1388. <https://doi.org/10.1093/cercor/bhq216>.
- Keysers, C., & Gazzola, V. (2009). Expanding the mirror: Vicarious activity for actions, emotions, and sensations. *Current Opinion in Neurobiology*, 19(6), 666–671. <https://doi.org/10.1016/j.conb.2009.10.006>.
- Kitzbichler, M. G., Henson, R. N., Smith, M. L., Nathan, P. J., & Bullmore, E. T. (2011). Cognitive effort drives workspace configuration of human brain functional networks. *Journal of Neuroscience*, 31(22), 8259–8270. <https://doi.org/10.1523/JNEUROSCI.0440-11.2011>.
- Koster-Hale, J., & Saxe, R. (2013). Theory of mind: A neural prediction problem. *Neuron*, 79(5), 836–848. <https://doi.org/10.1016/j.neuron.2013.08.020>.
- Lamm, C., Meltzoff, A. N., & Decety, J. (2010). How do we empathize with someone who is not like us? A functional magnetic resonance imaging study. *Journal of Cognitive Neuroscience*, 22(2), 362–376. <https://doi.org/10.1162/jocn.2009.21186>.
- Leslie, A. M., Friedman, O., & German, T. P. (2004). Core mechanisms in “theory of mind”. *Trends in Cognitive Sciences*, 8(12), 528–533. <https://doi.org/10.1016/j.tics.2004.10.001>.
- Lieberman, M. D. (2007). Social cognitive neuroscience: A review of core processes. *Annual Review of Psychology*, 58, 259–289. <https://doi.org/10.1146/annurev.psych.58.110405.085654>.
- Mar, R. A. (2011). The neural bases of social cognition and story comprehension. *Annual Review of Psychology*, 62, 103–134. <https://doi.org/10.1146/annurev-psych-120709-145406>.
- Margulies, D. S., Ghosh, S. S., Goulas, A., Falkiewicz, M., Huntenburg, J. M., Langs, G., ... Smallwood, J. (2016). Situating the default-mode network along a principal gradient of macroscale cortical organization. *Proceedings of the National Academy of Sciences*, 113(44), 12574–12579. <https://doi.org/10.1073/pnas.1608282113>.
- Mars, R. B., Neubert, F. X., Noonan, M. P., Sallet, J., Toni, I., & Rushworth, M. F. (2012a). On the relationship between the “default mode network” and the “social brain”. *Frontiers in Human Neuroscience*, 6, 189. <https://doi.org/10.3389/fnhum.2012.00189>.
- Mars, R. B., Sallet, J., Schüffelgen, U., Jbabdi, S., Toni, I., & Rushworth, M. F. S. (2012b). Connectivity-based subdivisions of the human right “temporoparietal junction area”: Evidence for different areas participating in different cortical networks. *Cerebral Cortex*, 22(8), 1894–1903. <https://doi.org/10.1093/cercor/bhr268>.
- Mazoyer, B., Zago, L., Mellet, E., Bricogne, S., Etard, O., Houdé, O., ... Tzourio-Mazoyer, N. (2001). Cortical networks for working memory and executive functions sustain the conscious resting state in man. *Brain Research Bulletin*, 54(3), 287–298. [https://doi.org/10.1016/s0361-9230\(00\)00437-8](https://doi.org/10.1016/s0361-9230(00)00437-8).
- Menon, V., & Uddin, L. Q. (2010). Saliency, switching, attention and control: A network model of insula function. *Brain Structure & Function*, 214(5–6), 655–667. <https://doi.org/10.1007/s00429-010-0262-0>.
- Mier, D., Lis, S., Neuthe, K., Sauer, C., Esslinger, C., Gallhofer, B., ... Kirsch, P. (2010a). The involvement of emotion recognition in affective theory of mind. *Psychophysiology*, 47(6), 1028–1039. <https://doi.org/10.1111/j.1469-8986.2010.01031.x>.
- Mier, D., Sauer, C., Lis, S., Esslinger, C., Wilhelm, J., Gallhofer, B., ... Kirsch, P. (2010b). Neuronal correlates of affective theory of mind in schizophrenia out-patients: Evidence for a baseline deficit. *Psychological Medicine*, 40(10), 1607–1617. <https://doi.org/10.1017/S0033291709992133>.
- Mitchell, J. (2009). Inferences about mental states. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1521), 1309–1316. <https://doi.org/10.1098/rstb.2008.0318>.
- Molenberghs, P., Cunnington, R., & Mattingley, J. B. (2009). Is the mirror neuron system involved in imitation? A short review and meta-analysis. *Neuroscience and Biobehavioral Reviews*, 33(7), 975–980. <https://doi.org/10.1016/j.neubiorev.2009.03.010>.
- Molenberghs, P., Cunnington, R., & Mattingley, J. (2011). Brain regions with mirror properties: A meta-analysis of 125 human fMRI studies. *Neuroscience and Biobehavioral Reviews*, 36, 341–349. <https://doi.org/10.1016/j.neubiorev.2011.07.004>.
- Molenberghs, P., Johnson, H., Henry, J. D., & Mattingley, J. B. (2016). Understanding the minds of others: A neuroimaging meta-analysis. *Neuroscience and Biobehavioral Reviews*, 65, 276–291. <https://doi.org/10.1016/j.neubiorev.2016.03.020>.
- Murray, R. J., Schaer, M., & Debbané, M. (2012). Degrees of separation: A quantitative neuroimaging meta-analysis investigating self-specificity and shared neural activation between self- and other-reflection. *Neuroscience and Biobehavioral Reviews*, 36(3), 1043–1059. <https://doi.org/10.1016/j.neubiorev.2011.12.013>.
- Naughtin, C. K., Horne, K., Schneider, D., Venini, D., York, A., & Dux, P. E. (2017). Do implicit and explicit belief processing share neural substrates? *Human Brain Mapping*, 38(9), 4760–4772. <https://doi.org/10.1002/hbm.23700>.
- Nijhof, A. D., Bardi, L., Brass, M., & Wiersma, J. R. (2018). Brain activity for spontaneous and explicit mentalizing in adults with autism spectrum disorder: An fMRI study. *NeuroImage: Clinical*, 18, 475–484. <https://doi.org/10.1016/j.nicl.2018.02.016>.
- Oakley, B. F., Brewer, R., Bird, G., & Catmur, C. (2016). Theory of mind is not theory of emotion: A cautionary note on the reading the mind in the eyes test. *Journal of Abnormal Psychology*, 125(6), 818. <https://doi.org/10.1037/abn0000182>.
- Osher, D. E., Saxe, R. R., Koldewyn, K., Gabrieli, J. D. E., Kanwisher, N., & Saygin, Z. M. (2016). Structural connectivity fingerprints predict cortical selectivity for multiple visual categories across cortex. *Cerebral Cortex*, 26(4), 1668–1683. <https://doi.org/10.1093/cercor/bhu303>.
- Passingham, R. E., Stephan, K. E., & Kötter, R. (2002). The anatomical basis of functional localization in the cortex. *Nature Reviews Neuroscience*, 3(8), 606–616. <https://doi.org/10.1038/nrn893>.
- Pehrs, C., Zaki, J., Schlottermeier, L. H., Jacobs, A. M., Kuchinke, L., & Koelsch, S. (2017). The temporal pole top-down modulates the ventral visual stream during social cognition. *Cerebral Cortex*, 27(1), 777–792. <https://doi.org/10.1093/cercor/bhw226>.
- Pehrs, C., Zaki, J., Taruffi, L., Kuchinke, L., & Koelsch, S. (2018). Hippocampal-temporopolar connectivity contributes to episodic simulation during social cognition. *Scientific Reports*, 8(1), 1–13. <https://doi.org/10.1038/s41598-018-24557-y>.
- Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences*, 1(4), 515–526. <https://doi.org/10.1017/S0140525X00076512>.
- Preston, S. D., & de Waal, F. B. M. (2002). Empathy: Its ultimate and proximate bases. *The Behavioral and Brain Sciences*, 25(1), 1–71. <https://doi.org/10.1017/s0140525x02000018>.
- Radua, J., Mataix-Cols, D., Phillips, M. L., El-Hage, W., Kronhaus, D. M., Cardoner, N., ... Surguladze, S. (2012). A new

- meta-analytic method for neuroimaging studies that combines reported peak coordinates and statistical parametric maps. *European Psychiatry*, 27(8), 605–611. <https://doi.org/10.1016/j.eurpsy.2011.04.001>.
- Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, G. L. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America*, 98(2), 676–682. <https://doi.org/10.1073/pnas.98.2.676>.
- Regenbogen, C., Habel, U., & Kellermann, T. (2013). Connecting multimodality in human communication. *Frontiers in Human Neuroscience*, 7. <https://doi.org/10.3389/fnhum.2013.00754>.
- Reiter, A. M. F., Kanske, P., Eppinger, B., & Li, S.-C. (2017). The aging of the social mind - differential effects on components of social understanding. *Scientific Reports*, 7(1), 1–8. <https://doi.org/10.1038/s41598-017-10669-4>.
- Rice, K., Moraczewski, D., & Redcay, E. (2016). Perceived live interaction modulates the developing social brain. *Social Cognitive and Affective Neuroscience*, 11(9), 1354–1362. <https://doi.org/10.1093/scan/nsw060>.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27(1), 169–192. <https://doi.org/10.1146/annurev.neuro.27.070203.144230>.
- Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, 3(2), 131–141. [https://doi.org/10.1016/0926-6410\(95\)00038-0](https://doi.org/10.1016/0926-6410(95)00038-0).
- Rothmayr, C., Sodian, B., Hajak, G., Döhl, K., Meinhardt, J., & Sommer, M. (2011). Common and distinct neural networks for false-belief reasoning and inhibitory control. *NeuroImage*, 56(3), 1705–1713. <https://doi.org/10.1016/j.neuroimage.2010.12.052>.
- Saygin, Z. M., Osher, D. E., Norton, E. S., Youssoufian, D. A., Beach, S. D., Feather, J., ... Kanwisher, N. (2016). Connectivity precedes function in the development of the visual word form area. *Nature Neuroscience*, 19(9), 1250–1255. <https://doi.org/10.1038/nn.4354>.
- Schilbach, L., Eickhoff, S. B., Mojzisch, A., & Vogeley, K. (2008). What's in a smile? Neural correlates of facial embodiment during social interaction. *Social Neuroscience*, 3(1), 37–50. <https://doi.org/10.1080/17470910701563228>.
- Schilbach, L., Timmermans, B., Reddy, V., Costall, A., Bente, G., Schlicht, T., ... Vogeley, K. (2013). Toward a second-person neuroscience. *Behavioral and Brain Sciences*, 36(4), 393–414. <https://doi.org/10.1017/S0140525X12000660>.
- Schippers, M. B., Gazzola, V., Goebel, R., & Keysers, C. (2009). Playing charades in the fMRI: Are mirror and/or mentalizing areas involved in gestural communication? *Plos One*, 4(8), e6801. <https://doi.org/10.1371/journal.pone.0006801>.
- Schippers, M. B., Roebroek, A., Renken, R., Nanetti, L., & Keysers, C. (2010). Mapping the information flow from one brain to another during gestural communication. *Proceedings of the National Academy of Sciences*, 107(20), 9388–9393. <https://doi.org/10.1073/pnas.1001791107>.
- Schurz, M., Radua, J., Aichhorn, M., Richlan, F., & Perner, J. (2014). Fractionating theory of mind: A meta-analysis of functional brain imaging studies. *Neuroscience and Biobehavioral Reviews*, 42, 9–34. <https://doi.org/10.1016/j.neubiorev.2014.01.009>.
- Schuerk, T., Döhl, K., Sodian, B., Keck, I. R., Rupprecht, R., & Sommer, M. (2014). Functional activity and effective connectivity of the posterior medial prefrontal cortex during processing of incongruent mental states. *Human Brain Mapping*, 35(7), 2950–2965. <https://doi.org/10.1002/hbm.22377>.
- Schuerk, T., Schurz, M., Müller, F., Rupprecht, R., & Sommer, M. (2017). The rTPJ's overarching cognitive function in networks for attention and theory of mind. *Social Cognitive and Affective Neuroscience*, 12(1), 157–168. <https://doi.org/10.1093/scan/nsw163>.
- Sebastian, C. L., Fontaine, N. M. G., Bird, G., Blakemore, S.-J., De Brito, S. A., McCrory, E. J. P., ... Viding, E. (2012). Neural processing associated with cognitive and affective Theory of Mind in adolescents and adults. *Social Cognitive and Affective Neuroscience*, 7(1), 53–63. <https://doi.org/10.1093/scan/nsr023>.
- Shamay-Tsoory, S. G., & Aharon-Peretz, J. (2007). Dissociable prefrontal networks for cognitive and affective theory of mind: A lesion study. *Neuropsychologia*, 45(13), 3054–3067. <https://doi.org/10.1016/j.neuropsychologia.2007.05.021>.
- Shamay-Tsoory, S. G., Aharon-Peretz, J., & Perry, D. (2009). Two systems for empathy: A double dissociation between emotional and cognitive empathy in inferior frontal gyrus versus ventromedial prefrontal lesions. *Brain*, 132(3), 617–627. <https://doi.org/10.1093/brain/awn279>.
- Shine, J. M., Bissett, P. G., Bell, P. T., Koyejo, O., Balsters, J. H., Gorgolewski, K. J., ... Poldrack, R. A. (2016). The dynamics of functional brain networks: Integrated network states during cognitive task performance. *Neuron*, 92(2), 544–554. <https://doi.org/10.1016/j.neuron.2016.09.018>.
- Shine, J. M., & Poldrack, R. A. (2018). Principles of dynamic network reconfiguration across diverse brain states. *NeuroImage*, 180, 396–405. <https://doi.org/10.1016/j.neuroimage.2017.08.010>.
- Shulman, G. L., Fiez, J. A., Corbetta, M., Buckner, R. L., Miezin, F. M., Raichle, M. E., & Petersen, S. E. (1997). Common blood flow changes across visual tasks: II. Decreases in cerebral cortex. *Journal of Cognitive Neuroscience*, 9(5), 648–663. <https://doi.org/10.1162/jocn.1997.9.5.648>.
- Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R. J., & Frith, C. D. (2004). Empathy for pain involves the affective but not sensory components of pain. *Science*, 303(5661), 1157–1162. <https://doi.org/10.1126/science.1093535>.
- Smith, S. M., Fox, P. T., Miller, K. L., Glahn, D. C., Fox, P. M., Mackay, C. E., ... Beckmann, C. F. (2009). Correspondence of the brain's functional architecture during activation and rest. *Proceedings of the National Academy of Sciences*, 106(31), 13040–13045. <https://doi.org/10.1073/pnas.0905267106>.
- Sommer, M., Döhl, K., Sodian, B., Meinhardt, J., Thoermer, C., & Hajak, G. (2007). Neural correlates of true and false belief reasoning. *NeuroImage*, 35(3), 1378–1384. <https://doi.org/10.1016/j.neuroimage.2007.01.042>.
- Sperduti, M., Guionnet, S., Fossati, P., & Nadel, J. (2014). Mirror neuron system and mentalizing system connect during online social interaction. *Cognitive Processing*, 15(3), 307–316. <https://doi.org/10.1007/s10339-014-0600-x>.
- Spunt, R. P., & Lieberman, M. D. (2012a). An integrative model of the neural systems supporting the comprehension of observed emotional behavior. *NeuroImage*, 59(3), 3050–3059. <https://doi.org/10.1016/j.neuroimage.2011.10.005>.
- Spunt, R. P., & Lieberman, M. D. (2012b). Dissociating modality-specific and supramodal neural systems for action understanding. *The Journal of Neuroscience*, 32(10), 3575–3583. <https://doi.org/10.1523/JNEUROSCI.5715-11.2012>.
- Steinbeis, N., Bernhardt, B. C., & Singer, T. (2015). Age-related differences in function and structure of rSMG and reduced functional connectivity with DLPPFC explains heightened emotional egocentricity bias in childhood. *Social Cognitive and Affective Neuroscience*, 10(2), 302–310. <https://doi.org/10.1093/scan/nsu057>.
- Stietz, J., Jauk, E., Krach, S., & Kanske, P. (2019). Dissociating empathy from perspective-taking: Evidence from intra- and inter-individual differences research. *Frontiers in Psychiatry*, 10. <https://doi.org/10.3389/fpsy.2019.00126>.
- Tavor, I., Jones, O. P., Mars, R. B., Smith, S. M., Behrens, T. E., & Jbabdi, S. (2016). Task-free MRI predicts individual differences in brain activity during task performance. *Science*, 352(6282), 216–220. <https://doi.org/10.1126/science.aad8127>.

- Tettamanti, M., Vaghi, M. M., Bara, B. G., Cappa, S. F., Enrici, I., & Adenzato, M. (2017). Effective connectivity gateways to the Theory of Mind network in processing communicative intention. *NeuroImage*, 155, 169–176. <https://doi.org/10.1016/j.neuroimage.2017.04.050>.
- Thioux, M., Suttrup, J., & Keyers, C. (2018). Perceiving hesitation requires both the motor and mentalizing systems. *BioRxiv*, 454298. <https://doi.org/10.1101/454298>.
- Timmers, I., Park, A. L., Fischer, M. D., Kronman, C. A., Heathcote, L. C., Hernandez, J. M., ... Simons, L. E. (2018). Is empathy for pain unique in its neural correlates? A meta-analysis of neuroimaging studies of empathy. *Frontiers in Behavioral Neuroscience*, 12. <https://doi.org/10.3389/fnbeh.2018.00289>.
- Titchener, E. B. (1909). *Lectures on the experimental psychology of the thought-process*. New York: MacMillan. <https://doi.org/10.1037/10877-000>.
- Torrsi, S. J., Lieberman, M. D., Bookheimer, S. Y., & Altshuler, L. L. (2013). Advancing understanding of affect labeling with dynamic causal modeling. *NeuroImage*, 82, 481–488. <https://doi.org/10.1016/j.neuroimage.2013.06.025>.
- Trautwein, F.-M., Singer, T., & Kanske, P. (2016). Stimulus-driven reorienting impairs executive control of attention: Evidence for a common bottleneck in anterior insula. *Cerebral Cortex*, 26(11), 4136. <https://doi.org/10.1093/cercor/bhw225>.
- Valk, S. L., Bernhardt, B. C., Böckler, A., Trautwein, F.-M., Kanske, P., & Singer, T. (2017). Socio-cognitive phenotypes differentially modulate large-scale structural covariance networks. *Cerebral Cortex*, 27(2), 1358–1368. <https://doi.org/10.1093/cercor/bhw319>.
- Van Ackeren, M. J., Smaragdi, A., & Rueschemeyer, S.-A. (2016). Neuronal interactions between mentalising and action systems during indirect request processing. *Social Cognitive and Affective Neuroscience*, 11(9), 1402–1410. <https://doi.org/10.1093/scan/nsw062>.
- Van Overwalle, F. (2009). Social cognition and the brain: A meta-analysis. *Human Brain Mapping*, 30(3), 829–858. <https://doi.org/10.1002/hbm.20547>.
- Van Overwalle, F., & Baetens, K. (2009). Understanding others' actions and goals by mirror and mentalizing systems: A meta-analysis. *NeuroImage*, 48(3), 564–584. <https://doi.org/10.1016/j.neuroimage.2009.06.009>.
- Van Overwalle, F., & Vandekerckhove, M. (2013). Implicit and explicit social mentalizing: Dual processes driven by a shared neural network. *Frontiers in Human Neuroscience*, 7, 560.
- Van Overwalle, F., Van de Steen, F., & Mariën, P. (2019). Dynamic causal modeling of the effective connectivity between the cerebrum and cerebellum in social mentalizing across five studies. *Cognitive, Affective & Behavioral Neuroscience*, 19(1), 211–223. <https://doi.org/10.3758/s13415-018-00659-y>.
- Van den Heuvel, M. P., & Sporns, O. (2013). An anatomical substrate for integration among functional networks in human cortex. *Journal of Neuroscience*, 33(36), 14489–14500. <https://doi.org/10.1523/JNEUROSCI.2128-13.2013>.
- Vatansever, D., Menon, D. K., Manktelow, A. E., Sahakian, B. J., & Stamatakis, E. A. (2015). Default mode dynamics for global functional integration. *The Journal of Neuroscience*, 35(46), 15254–15262. <https://doi.org/10.1523/JNEUROSCI.2135-15.2015>.
- Wendelken, C., Ferrer, E., Whitaker, K. J., & Bunge, S. A. (2016). Fronto-parietal network reconfiguration supports the development of reasoning ability. *Cerebral Cortex*, 26(5), 2178–2190. <https://doi.org/10.1093/cercor/bhv050>.
- Wen, X., Liu, Y., Yao, L., & Ding, M. (2013). Top-down regulation of default mode activity in spatial visual attention. *The Journal of Neuroscience*, 33(15), 6444–6453. <https://doi.org/10.1523/JNEUROSCI.4939-12.2013>.
- Wig, G. S., Schlaggar, B. L., & Petersen, S. E. (2011). Concepts and principles in the analysis of brain networks. *Annals of the New York Academy of Sciences*, 1224(1), 126–146. <https://doi.org/10.1111/j.1749-6632.2010.05947.x>.
- Winter, K., Spengler, S., Bermpohl, F., Singer, T., & Kanske, P. (2017). Social cognition in aggressive offenders: Impaired empathy, but intact theory of mind. *Scientific Reports*, 7(1), 1–10. <https://doi.org/10.1038/s41598-017-00745-0>.
- Wolf, I., Dziobek, I., & Heekeren, H. R. (2010). Neural correlates of social cognition in naturalistic settings: A model-free analysis approach. *NeuroImage*, 49(1), 894–904. <https://doi.org/10.1016/j.neuroimage.2009.08.060>.
- Yeo, B. T. T., Krienen, F. M., Sepulcre, J., Sabuncu, M. R., Lashkari, D., Hollinshead, M., ... Buckner, R. L. (2011). The organization of the human cerebral cortex estimated by intrinsic functional connectivity. *Journal of Neurophysiology*, 106(3), 1125–1165. <https://doi.org/10.1152/jn.00338.2011>.
- Zaki, J., Ochsner, K. N., Hanelin, J., Wager, T. D., & Mackey, S. C. (2007). Different circuits for different pain: Patterns of functional connectivity reveal distinct networks for processing pain in self and others. *Social Neuroscience*, 2(3–4), 276–291. <https://doi.org/10.1080/17470910701401973>.
- Zaki, J., Weber, J., Bolger, N., & Ochsner, K. (2009). The neural bases of empathic accuracy. *Proceedings of the National Academy of Sciences*, 106(27), 11382–11387. <https://doi.org/10.1073/pnas.0902666106>.
- Zhou, Y., Friston, K. J., Zeidman, P., Chen, J., Li, S., & Razi, A. (2018). The hierarchical organization of the default, dorsal attention and salience networks in adolescents and young adults. *Cerebral Cortex*, 28(2), 726–737. <https://doi.org/10.1093/cercor/bhx307>.