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DOI:

[10.1016/j.neuropsychologia.2016.07.030](https://doi.org/10.1016/j.neuropsychologia.2016.07.030)

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Document Version

Peer reviewed version

Citation for published version (Harvard):

Eddy, CM 2016, 'The junction between self and other? Temporo-parietal dysfunction in neuropsychiatry', *Neuropsychologia*, vol. 89, pp. 465-477. <https://doi.org/10.1016/j.neuropsychologia.2016.07.030>

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Checked 28/9/2016

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The junction between self and other?
Temporo-parietal dysfunction in neuropsychiatry

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Running title: Temporo-parietal dysfunction in neuropsychiatry

Word count: 8,388

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ABSTRACT

The temporo-parietal junction (TPJ) is implicated in a variety of processes including multisensory integration, social cognition, sense of agency and stimulus-driven attention functions. Furthermore, manipulation of cortical excitation in this region can influence a diverse range of personal and interpersonal perceptions, from those involved in moral decision making to judgments about the location of the self in space. Synthesis of existing studies places the TPJ at the neural interface between mind and matter, where information about both mental and physical states is processed and integrated, contributing to self-other differentiation. After first summarising the functions of the TPJ according to existing literature, this narrative review aims to offer insight into the potential role of TPJ dysfunction in neuropsychiatric disorders, with a focus on the involvement of the right TPJ in controlling representations relating to the self and other. Problems with self-other distinctions may reflect or pose a vulnerability to the symptoms associated with Tourette syndrome, Schizophrenia, Autistic Spectrum Disorder and Obsessive Compulsive Disorder. Further study of this most fascinating neural region will therefore make a substantial contribution to our understanding of neuropsychiatric symptomatology and highlight significant opportunities for therapeutic impact.

Agency; multisensory integration; social cognition; temporo-parietal junction

1. Functions of the temporo-parietal junction

The temporoparietal junction (TPJ, **Figure 1**) is a functionally defined region encompassing an area of cortex around the inferior parietal lobe, lateral occipital cortex, and posterior superior temporal sulcus (Mars et al., 2012). Anatomically, the TPJ has structural connections to areas including prefrontal cortex (Mesulam & Geshwind, 1978), cingulate gyrus (Chafee & Goldman-Rakic, 2000), premotor cortex (Rushworth et al., 2006) putamen and thalamus (Kucyi et al., 2012). The arcuate fasciculus and subcomponent III of the superior longitudinal fasciculus connect the TPJ and inferior frontal gyrus (Schmahmann et al., 2007; Umarova et al., 2010). TPJ connections to lateral and medial temporal areas include hippocampus and parahippocampus (Clower et al., 2001; Rockland et al., 2001; Seltzer & Pandya, 1984). Furthermore, some of these pathways may demonstrate hemispheric asymmetry, such as tracts along the extreme capsule which connect the TPJ to the insula (Kucyi et al., 2012).

The wealth of literature on TPJ function spans sensory, cognitive, emotional, social and motor domains, reflecting involvement in processes that contribute to our experience of both the external material world, derived through automatic awareness of sensory feedback; and the internal mental world, defined by transient emotional states and motivations. In sum, TPJ functions appear to underpin both mental and physical aspects of the self. TPJ dysfunction could therefore have a range of detrimental effects on conscious human experience and impact mental health. The focus of this narrative review reflects the emerging interest in the contribution of the right TPJ to the control of representations that differentiate between self and other. A brief introduction first highlights areas of research linked to the TPJ which may contribute to self-other judgments: multisensory processing, action imitation, sense of agency, attention and Theory of Mind (ToM): reasoning about mental states such as beliefs, intentions and emotions. Literature relating to TPJ subdivisions and lateralisation is then summarised. Discussion thereafter is centred on application of self-other distinction and related experimental observations to the understanding of symptoms in neuropsychiatric disorders, with a view to promoting discussion around the role of the TPJ in health and disease, and offering timely and novel hypotheses to stimulate further research. Studying conditions thought to involve TPJ dysfunction could highlight novel links between brain structure and function, as well as offering insight into the ontogenetic and neurodevelopmental aspects of this region, and the wider influence of TPJ involvement in healthy cortical networks.

1.1 Multisensory integration

The TPJ is an area of convergence for somatosensory, auditory and visual evoked responses (Matsushashi et al., 2004) and involved in sensorimotor integration (Blanke & Mohr, 2005). Studies of multisensory integration frequently refer to the concepts of bodily self-consciousness and physical embodiment (see Blanke et al., 2015; Longo et al., 2008). Multisensory information is combined to give the feeling of bodily self-consciousness, and being a unified entity (Ionta, Gassert & Blanke, 2011) localised at a certain position in space (Ionta et al., 2011). If this process breaks down, or the mental and physical aspects of the self are poorly integrated, this may result in out of body experiences (e.g. Blanke & Arzy, 2005).

Blanke et al. (2005) showed that transcranial magnetic stimulation (TMS) of the TPJ region can selectively impair the ability to imagine relocation of the self. Participants completed a task which involved making decisions about whether a glove was on the left or right hand of a figure, versus the left or right side of a computer screen. Comparisons with a task which involved rotating letters indicated that TPJ stimulation specifically affected own body re-orienting. More recently, Limanowski and Blankenburg (2015) showed increased activity in the TPJ was associated with decreased sense of body part ownership. Furthermore, TMS to the right TPJ can eliminate the effect of competing sensory information implying a role in the detection of inter-sensory conflict (Papeo et al., 2010). In sum, the TPJ underpins processes necessary for the perception of being mentally and physically in a single spatial location. These perceptions influence judgments relating to embodiment (Arzy et al., 2006) and self-other distinctions (van der Meer et al., 2011; Vogeley et al., 2001).

1.2 Control of imitation

Non-verbal imitation of conspecifics appears innate and automatic (Chartrand & Bargh, 1999) and is a context within which the distinction between self and other may become blurred. This ability may involve mirror neurons, which respond to both observation of another person performing a particular action and self-execution of that same action (Rizzolatti & Craighero, 2004). While the human mirror neuron system is thought to include premotor, posterior parietal and inferior frontal cortices (e.g. Plato Bello et al., 2015; Cerri et al., 2015), right TPJ is frequently active during imitation tasks that likely recruit mirror neurons. For example, one study found increased activity of right superior temporal sulcus extending to TPJ during trials in which the spatial mapping between observed and executed hand movements complicated the participants' task (Mengotti et al., 2012).

Shared representations, which contribute to behaviours such as imitation, may be the 'default-state' of the sensorimotor system (Brass et al., 2009). Spengler et al. (2010) found that TPJ lesions can impair the ability to suppress non-adaptive imitation. Furthermore, the ability to inhibit imitative responses was correlated with self-reported cognitive perspective taking (i.e. the tendency to put oneself in the position of another person). In addition, Santiesteban et al. (2015)^a found that electrical stimulation over left or right TPJ can modulate participants' performance on both imitation inhibition and perspective taking tasks. Imitation inhibition involves exerting control over a shared representational system which may be similarly activated for the same actions and perhaps mental states (e.g. physical viewpoints) in both the self and others. This system could help us appreciate the goals of observed actions, and therefore actor intentions, perhaps in addition to more basic physical expressions of emotion (see Sperduti et al., 2014; Keysers & Gazzola, 2014).

1.3 Sense of agency

Perceiving a coherent self which can be separated from others will impact sense of agency (SoA), i.e. perceptions about whether the self is the cause of experienced actions and sensory effects. A physically coherent self will at least partly rely on multi-sensory and sensorimotor integration, while a mentally coherent self may involve integration of mental states with physical self. SoA may be subdivided into automatic identification of actions as our own, and more conscious judgments of agency (Jeannerod, 2009). The automatic level allows for online action control. The forward model of motor control (Wolpert, 1995) holds that judgments about whether an action is as planned are based on whether the incoming sensorimotor information matches the original predicted state. The movement is perceived as self-generated only if reafferent signals match the expectation of the internal model (Jeannerod, 2009). When visual feedback is involved, agency judgments for actions may rely on perception-action coupling within the TPJ (Ro et al., 1998). The conscious level of agency judgment provides information about the actor's goals or mental state (Jeannerod, 2009) and may implicate prefrontal cortical regions (e.g. Miele et al., 2011). Therefore on the conscious level, SoA is linked to ToM (see 1.4 below).

One fMRI study of simple movements in healthy subjects (Frith & Farrer, 2002) found that comparison of the other-agent condition with the self-agent condition revealed activation in bilateral angular gyrus, left lateral premotor cortex, and precuneus. The TPJ may detect sensory incongruence, acting as an internal comparator for SoA judgments (Frith et al., 2000), with greater activity in association with greater incongruence between predicted action effects and actual sensory feedback (e.g. Spengler et al., 2010). A whole brain

quantitative meta-analysis (Sperduti et al., 2011) found converging activations in regions including the TPJ, pre-supplementary motor area, precuneus and dorsomedial prefrontal cortex when attributing agency to others, while insula activation was related to perceiving the self as the agent. Finally, lateralisation effects have been reported which imply that left inferior parietal activations are greater for first- versus third-person perspective (Ruby & Decety, 2001) and when the self is perceived as an acting agent rather than another person (Chaminade & Decety, 2002).

1.4 Theory of mind

The TPJ is active during a range of ToM tasks when a subject attempts to relate to the mental state of another (Schurz et al., 2014), including reasoning about beliefs and emotions (Corradi-Dell'Acqua et al., 2014), and during spontaneous perspective taking (Schurz et al., 2015). Between 5 and 12 years of age, TPJ activations become less generally associated with stories about people's mental states, appearances or actions, to being more specifically linked to reasoning about thoughts and emotions (Gweon et al., 2012). Importantly, right TPJ dysfunction may influence moral reasoning. Young et al. (2009) found that disrupting activity within this region via TMS led to intended harmful behaviours with neutral outcomes being rated as less morally wrong than without TMS. This appears to reflect greater dependence on the consequences of acts rather than the actor's mental state (or a relative suppression of ToM) when making a moral judgment.

It has been suggested that right TPJ plays a specific role in understanding a story character's false belief (Saxe & Kanwisher, 2003; Saxe & Wexler, 2005) which contrasts with reality and the belief of the test subject about e.g. the location of an object. Indeed, TPJ activity is significantly greater during false belief reasoning than when reasoning about other kinds of false representations e.g. false photographs (Saxe, 2010). Such a distinction may not be as apparent for left TPJ (Perner et al., 2006), although recent studies do support a role for the left TPJ in visual perspective taking (e.g. Santiesteban et al., 2015a) and humour appreciation (Slaby et al., 2015). One recent meta-analysis (Schurz et al., 2014) highlighted task related differences within the TPJ. More dorsal/posterior regions showed stronger activation for tasks involving covert or abstract mental states (false beliefs, trait judgments), whereas anterior/ventral activation was greater for tasks involving visible mental states (social animations, facial expressions, actions).

1.5 Attention

The TPJ may be part of a ventral attention system, central to stimulus-driven re-orienting of attention (Corbetta et al., 2008). This network, which may also involve the right inferior frontal gyrus, registers salient events in the visual, tactile and auditory modalities (Downar et al., 2000). For example, the degree of activation in right TPJ appears to provide a signal about the emergence of a target over time during visual search (Mavritsaki et al., 2010; Chechlacz et al., 2013), perhaps driven by incongruent or salient features. Attention functions can explain why right TPJ damage can result in visual neglect (Ptak & Schneider, 2011). Representational neglect involves an inability to imagine oneself in a particular location, or describe it from different visual perspectives (Bisiach & Luzzatti, 1978). The sensory integration functions of the TPJ are likely to explain why right TPJ lesions can impair visual imagery linked to navigation and autobiographical memory. In representational neglect, impaired visualization of first-person visual perspective may occur when posterior right TPJ lesions result in disconnection between intact environmental maps, egocentric spatial coding and visuospatial working memory or attention processes (Committeri et al., 2015). Given that such visual imagery and perspective taking may make an important contribution to tasks involving social cognition, assessing the performance of neglect patients on such tasks could offer insight into the interplay between visuospatial attention, mental imagery and ToM.

These proposed attention functions pose a significant challenge to the initial position of Saxe (2010) on the specificity of right TPJ to false belief reasoning. In fact, Mitchell (2008) reported overlapping right TPJ activity during an attention task involving the cueing of mislocations for target stimuli, and on a ToM task involving pictures, in healthy participants. However, as raised by Corbetta et al. (2008), colocalization of activations from ToM and reorienting paradigms does not necessarily imply a common process. Colocalization is only approximate, and given that activations are averaged over large cell populations, the observed distributions may actually have been slightly different (e.g. see **Figure 1**). Indeed, colocalization could obscure small systematic differences in the voxelwise distributions of the activations (Downing et al., 2007).

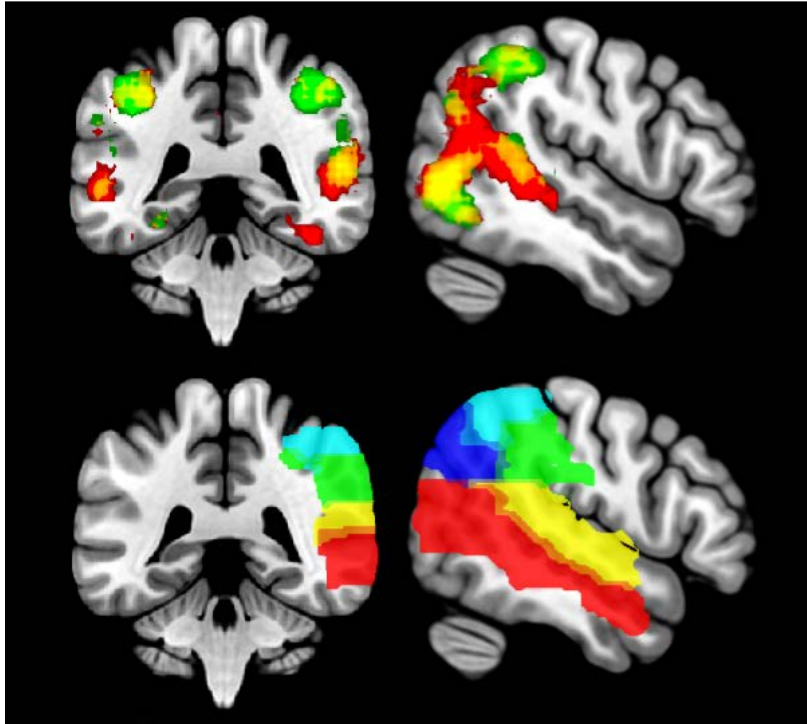


Figure 1. Anatomical and functional subdivisions of the temporo-parietal junction

Top row: Functional MRI meta-analysis data taken from *Neurosynth*, January 2016. Showing forward inference data identified using the terms 'social' in red, and 'attention' in green, with overlap in yellow. Bottom row: Standard anatomical maps using Automated Anatomical Labeling. Showing right inferior parietal lobe (cyan), supramarginal gyrus (green), angular gyrus (deep blue), superior temporal gyrus (yellow) and middle temporal gyrus (red). MNI co-ordinates 51, -41, 11. Created in MRICroGL.

2. Integrating perspectives on the role of the TPJ

The observed patterns across studies have motivated numerous integrative accounts seeking to clarify the overarching function of the TPJ. This section will summarise studies investigating subdivisions and lateralisation effects, before outlining evidence that the right TPJ may have a specific role in the control of representations related to the self and other.

2.1 *Temporo-parietal subdivisions and lateralisation effects*

One early proposal held the TPJ as a unitary region underpinning social cognition (Saxe & Wexler, 2005), although overlapping areas of activation in attention cueing paradigms (Mitchell et al., 2008; Aichorn et al., 2009) weaken this domain specific argument. It is likely that ToM is at least partially reliant on low-level computational processes (e.g. attention switching) which aid in the prediction of external events (Decety and Lamm, 2007). More specifically, the TPJ may play a general role in the determination of contextually appropriate

adaptive behaviours through the updating of internal models about the current environmental context based on incoming sensory information (Geng & Vossel, 2013). The nexus model of Carter and Huettel (2013) holds that multiple processing streams involved in social cognition, attention, memory, language and sensory processes converge within the TPJ to perform complex tasks involved in adaptive decision making. This latter proposal is in fitting with evidence for subdivisions within TPJ.

In addition to overlapping activation for attention and ToM, Scholz et al. (2009) identified two distinct regions with the right TPJ. One more inferior region was found to activate specifically during ToM tasks, while a more superior area was more specifically recruited during attention tasks. Other studies have used techniques such as diffusion weighted imaging, tractography based parcellation and resting state functional connectivity to identify two or three separate areas within right TPJ specifically (e.g. Bzdok et al., 2013; Mars et al., 2012). There is also evidence that networks involving these subdivisions of TPJ can activate antagonistically, and this has been proposed to reflect internally versus externally oriented attention (Bzdok et al., 2013). For example, Kubit and Jack (2013) propose that mentalizing and internally directed attention are linked to posterior right TPJ, which deactivates the neighbouring anterior portion, which in turn usually directs attention towards salient external stimuli. In this way the right TPJ may therefore allow shifting or switching between social and non-social processing. In summary, studies suggest that more posterior and dorsal parts of right TPJ (i.e. angular gyrus) seem to be associated with processing social information and co-activate with other brain regions thought to be involved in ToM. More anterior and ventral parts of the right TPJ may be engaged by other types of information during non-social tasks that require externally cued attention.

An important issue is the question of how much TPJ function is lateralised. As mentioned previously, left inferior parietal activations are greater when the self is perceived as an acting agent whereas right side activations are greater in the context of other-agent attributions (Chaminade and Decety, 2002). Similarly, right and left inferior parietal regions respond differentially in healthy participants to motor imagery from the first and third person perspective (Ruby & Decety, 2001). Therefore the balance of activity across hemispheres in the TPJ may contribute to self-other differentiation.

Structural connectivity studies have also indicated hemispheric asymmetries in the strength of connections involving the TPJ. Kucyi et al. (2012) investigated connections between TPJ and brain regions thought to be involved in the right ventral attention network (i.e. insula and inferior frontal gyrus) in addition to areas linked to salience or pain processing (putamen, cingulate, thalamus). One finding was a leftward asymmetry in the strength of connections between the TPJ and inferior frontal gyrus, which may reflect language lateralisation. Of greater interest, they identified a rightward asymmetry in the

strength of connectivity between the TPJ and insula in healthy participants, which was strongest in females. Such findings appear in accordance with reported lateralisation effects in some functional imaging studies. For example, stimuli that elicit automatic affective responses (e.g. unattended emotional facial expressions), can lead to greater right hemisphere activations involving TPJ (e.g. Inuggi et al., 2014). These studies highlight complex interactions between emotion, attention and lateralisation.

Another study (Igelstrom et al., 2015) reported four bilaterally-symmetrical subdivisions (one right-side biased), after using independent components analysis on resting state data studies. One area was connected to sensori-motor regions and one to the auditory cortex. Two sub-regions presented as left and right biased independent components and were associated with frontoparietal activation, or social/default mode networks. The more posterior TPJ cluster associated with social functions showed mirrored networks on the left and right side with reciprocal connections, which the authors suggest are consistent with the notion of related but distinct functions of left and right posterior TPJ. Indeed, a meta-analysis conducted by Schurz et al. (2013) provided evidence that the left, but not the right, TPJ was associated with a domain general function of representing different spatial perspectives linked to both reasoning about false belief and more general visual perspective taking (e.g. imaging viewing objects from a different angle). More recently, Santiesteban et al. (2015)b found that transcranial direct current stimulation (tDCS) of the right or left TPJ modulates performance on both action imitation inhibition and visual perspective taking tasks. If there are subdivisions within the TPJ, then it is possible that conflicting results across studies relating to lateralisation effects could reflect the effects of targeting different subdivisions.

2.2 A role for the right TPJ in the control of self-other representations

Multisensory integration and action imitation involve the physical self, whereas other TPJ functions such as social cognition and SoA involve the mental aspect of the self. An overarching role for the right TPJ in the control of neural representations pertaining to the self or other may therefore comprise a straightforward account for many study findings, including those linked to false belief. In the false belief task, not only is there a mismatch between a story protagonist's mental state and reality, but also between the story protagonist's belief and test subject's belief. Therefore an alternative explanation for greater TPJ activations in association with false belief versus false photo conditions is that the former are more closely linked to self-other distinctions.

One phenomenon in which self and other representations are particularly relevant is mirror-touch synaesthesia: a condition whereby the subject feels a tactile sensation on their own body when observing another person being touched. Using a motor imitation task, Santiesteban et al. (2015)^b showed that this condition is associated with greater motor interference when these individuals perform a movement which is incongruent with the movement they observe performed by another person. As greater self and other blending could contribute to this interference, it is interesting that people with mirror-touch synaesthesia can exhibit decreased grey matter in right angular gyrus in comparison to healthy controls (Holle et al., 2013). In fact, anodal tDCS of right TPJ can enhance both control over imitation, and visual perspective taking, although not the ability to attribute mental states to self or other (Santiesteban et al., 2012). These findings are supported by the work of Giardina et al. (2015), who found evidence that repetitive TMS of the right TPJ influenced self-other motor representations; and Hogeveen et al. (2015), who clarified that while right TPJ stimulation helped the participant to resist motor imitation, there was no effect on general inhibitory ability or ToM. In sum the right TPJ appears to underpin the domain general control of self and other representations, which can be independent of ToM. Right TPJ activations may emphasise the incongruence between self and other, or allow for switching between these representations (e.g. Sowden & Catmur, 2015). De-coupling the self and other may aid higher level perspective taking because another person's mental state will frequently conflict with one's own. Furthermore, the identification of a mental state specific to the self allows the self to be seen as an independent agent, linking self-other differentiation to ToM and SoA.

If right TPJ supports control of self-other representations in general, this could explain the findings of many studies involving reasoning bias linked to social groups (see Sowden & Shah, 2014). Cheng et al. (2010) used fMRI to study participants observing strangers and close others experiencing a painful stimulus, and found that the closer the relationship between the observer and the person experiencing the pain, the greater the right TPJ deactivation. This deactivation may indicate increased self-other blending which aids empathy towards close others. A recent TMS study targeted the right TPJ and explored the effect on outgroup punishment behaviours (Baumgartner et al., 2014). At baseline, a reduced tendency to take the perspective of outgroup versus ingroup members was linked to retaliation and parochial punishment. However, TMS to the right TPJ reduced this difference in treatment between ingroup and outgroup members perhaps reflecting a reduction in self-ingroup other-outgroup differentiation.

Overall, the evidence for the self-other differentiation account is compelling and this theory provides a useful framework for interpreting the findings of many studies. However, it may be argued that further work is needed to determine that such a decoupling mechanism

is indeed specialized for application within the social domain, and is not involved in more general processing related to the degree of congruence or incongruence between different streams of sensory stimuli. Indeed, it is not clear how independent self-other decoupling is from processes that integrate the mental and physical aspects pertaining only to the self-representation i.e. is 'other' attribution simply a failure of the integration process?

3. The relevance of TPJ dysfunction in clinical neuropsychiatry

Previous sections have proposed a central role for the right TPJ in the control of self-other representations, which will contribute to judgments about both the physical and mental self. A physical sense of self may rely on sensory congruence, while mental sense of self may require awareness of own mental states. Successful cognitive perspective taking requires an ability to differentiate between the mental aspects of the self and others, while determining the agent of an act relies upon differentiation between sensory stimuli which pertain to actions made by the physical self, versus those that do not. However, it may also be important to achieve congruence between the mental (i.e. thoughts and intentions) and physical (i.e. actions and sensory feedback) aspects of one's self. This section explores how TPJ dysfunction may contribute to neuropsychiatric symptomatology. Difficulties with self and other representations could explain some common features of Tourette syndrome, schizophrenia, Autistic Spectrum Disorders and Obsessive Compulsive Disorder (**Table 1**).

3.1 Tourette syndrome

Tourette syndrome (TS) is a neurodevelopmental disorder involving tics: repetitive movements and vocalisations. Existing models propose that tics occur when specific groups of striatal neurons are inappropriately activated and inhibit basal ganglia output neurons, which then disinhibit movement pattern generators in the cortex (Albin & Mink, 2006). Support for basal ganglia dysfunction comes from numerous studies (e.g. Peterson et al., 1993; Singer et al., 1993; Bloch et al., 2005). However, the precise locus of tic generation remains to be determined (Worbe et al., 2015). Moreover, the complexity and context dependent nature of some tics, such as socially inappropriate urges and mirroring tics (echophenomena), implicate wider cortical involvement (Eddy & Cavanna, 2014b).

The first functional imaging study to emphasise the potential importance of the right TPJ (Eddy et al., submitted) explored activation in adults with TS versus healthy controls during a perspective taking task. This investigation found that TS was associated with reduced activation within right TPJ, and more specifically, greater hypoactivation of the right

supramarginal gyrus was linked to more echophenomena. Taking this finding together with evidence that right TPJ activation is associated with self-other differentiation, and is needed to avoid imitation (e.g. Spengler et al., 2010), TS may involve difficulties with self-other differentiation, which in turn contributes to mirroring tics.

Tics are characteristically preceded by a sensory-cognitive premonitory urge (feeling like pressure, or an itch) that the patient finds hard to resist. Activation of right angular gyrus within the TPJ can be strongly associated with the severity of urges to tic (Eddy et al., submitted). This could indicate that problems with multisensory or sensorimotor integration contribute to premonitory urges. Perhaps performing a tic leads to relief for a short time because when the tic is performed, motor and sensory feedback become congruent, helping maintain a coherent physical self. Another possibility is that the problem of merging self and other representations may prompt the patient to acquire a greater degree of congruent sensory feedback, to maintain a stable representation of the physical self. This could further help to explain the tendency of patients to seek other forms of sensory congruence (e.g. complex tics involving both somatosensory and visual feedback, and ‘just-right’ experiences whereby the patient has a conscious compulsion to act until achieving a particular sensory state: see Eddy & Cavanna, 2014b). A further advantage of concordant sensory feedback could be to help maintain healthy SoA. Disrupted SoA could lead to further behavioural problems, including impulse control disorders, which are frequent in TS (e.g. Wright et al., 2012). That is, poor integration between physical acts of the self and awareness of one’s own mental states could lead one to ‘act without thinking’.

The merging of self and other may impair more complex abstract reasoning related to ToM when oneself and the other hold conflicting perspectives (e.g. Spengler et al., 2010). This could help explain why patients with TS have been shown to make errors on ToM tasks (e.g. Eddy et al., 2010a&b; Eddy et al., 2011), particularly when required to reason about conflicting mental states (Eddy & Cavanna, 2013). In addition, it was recently found that people with TS exhibit increased personal distress when seeing other people in emotionally upsetting circumstances, despite reporting less perspective taking in everyday life (Eddy et al., 2015). While increased self-other blending may enhance empathy, one down-side may be difficulty in controlling one’s own emotional reactions and in maintaining clear self-other distinctions needed for abstract perspective taking.

It is important to further consider the dissociation between personal distress and cognitive perspective taking. One possibility is that reduced perspective taking in TS is a coping strategy, motivated by uncomfortable experiences involving increased personal upset due to emotion contagion from others in distress (Eddy et al., 2015). However, an alternative explanation is based on the different types of ToM tasks used in studies. Some tasks involve visual cues and relatively automatic empathic responses (e.g. imitation, emotion contagion,

recognising non-verbal expressions), and are therefore likely to rely on a degree of overlap between self and other representations. However, verbal tasks involving abstract perspective taking (e.g. imagine another person's visual perspective, or understand their false belief) require clearer differentiation between the self and the other, as the self-representation is associated with misinformation or conflicting mental content. Problems with right TPJ based decoupling could help explain the behavioural pattern reported in TS, and why patients with right TPJ lesions exhibit both a stronger tendency to blend with others (as evidenced by poorer imitation-inhibition) and less cognitive perspective taking than healthy controls (Spengler et al., 2010).

Evidence for over-application of ToM based on visual cues was recently reported in TS, whereby these patients spontaneously attributed mental states to randomly moving shapes when healthy controls did not (Eddy & Cavanna, 2015). This supports the possibility of an increased sensitivity to some forms of sensory stimuli in TS whereby non-social stimuli may be perceived as socially salient. An increased sensitivity to non-verbal social cues may also help to explain why patients can experience urges to carry out problematic social behaviours to e.g. to insult other people (Kurlan et al., 1996; Eddy & Cavanna, 2013). Patients who have such urges are usually aware of the potential problems their actions will lead to (e.g. offence) and while the patient has no negative intent, this awareness seems to lead to an ironic desire to perform the socially inappropriate behaviours. It is possible that socially inappropriate behaviours arise from an urge to achieve mental self-other decoupling: a socially inappropriate act reflects incongruence between the mental states of victim and perpetrator. Furthermore, as increased personal distress is most apparent in TS patients who report fewer tics (Eddy et al., 2015), tics could reduce self-other blending in empathic situations, perhaps by increasing salience of mental or physical aspects relating to the self.

3.2 Schizophrenia

Over time, patients with first-episode psychosis show progressive loss of grey matter volume in frontal, temporal and parietal regions when compared with healthy controls, with temporal lobes primarily affected in chronic schizophrenia (Vita et al., 2012). Current models highlight the importance of both hippocampus and the TPJ in psychotic symptoms (Wible, 2012), and functional disconnection between auditory temporal areas and frontal structures in the development of auditory hallucinations (Mou et al., 2013). However, abnormalities in right TPJ structure (e.g. sulcal morphology: Plaze et al., 2015) and resting functional connectivity

(e.g. reduced functional connectivity between bilateral TPJ and precuneus at rest: Zhang et al., 2014) have been highlighted in these patients.

It has been suggested that hyper-ToM may occur in schizophrenia (Abu-Akel & Bailey, 2000) and could contribute to the development of psychosis and paranoia (e.g. Walston et al., 2000). However, the findings of social cognition studies in schizophrenia have been mixed. Some studies have found patients with schizophrenia can over-attribute intentionality to inanimate objects (e.g. Russell et al., 2006). However, others have reported hypo-mentalising. For example, Das et al. (2012), showed that when viewing animations that depicted social interactions prompting ToM versus random movement, people with schizophrenia showed evidence of reduced attribution of intentions and less appropriate interpretation of the animations overall, plus evidence of right superior temporal dysfunction. Similarly, Hashimoto et al. (2014) reported similar brain activations for stimuli depicting biological motion and scrambled motion in patients with schizophrenia while differential activation was apparent in controls, while Walter et al. (2009) reported hypoactivation within the paracingulate and bilateral TPJ in paranoid schizophrenia during a ToM task which featured contrasting conditions involving physical causation versus intended human actions. Overall, multiple factors could be responsible for the variations in study results, including the prevalence of paranoia in each sample, patterns of neural atrophy, or medication use.

One reported pattern is that people with schizophrenia can exhibit impairment on cognitive perspective taking tasks despite higher scores on emotional empathy measures than controls (e.g. Bora et al., 2008; Lombardo et al., 2007; Shamay-Tsoory et al., 2007). Lehmann et al. (2014) found that in comparison to healthy controls, people with schizophrenia reported more often experiencing overwhelming emotions, lack of emotion, negative emotional contagion and symbolization of emotion by imagination. Interestingly, these patients were more likely to rely on bodily expression of emotion rather than more abstract aspects linked to mentalising. In addition, McCormick et al. (2012), reported that people with psychotic symptoms exhibit greater mirror neuron system activity than healthy controls during observations of other people's hand movements. Like people with TS (Eddy & Cavanna, 2015) and patients with right TPJ lesions (Spengler et al., 2010), patients with schizophrenia can show increased personal distress i.e. greater resonance with the negative affective state of others, despite reduced cognitive perspective taking (Haker et al., 2012; McCormick et al., 2012). Such findings could imply increased self-other blending in some patients, which can enhance empathic processes but impair mental state reasoning on tasks when the perspectives of self and other need to be distinct.

Elevated personal distress can be apparent before the onset of deficits in cognitive perspective taking in schizophrenia (Achim et al., 2011). This raises the possibility of compensation effects. For example, Brüne et al. (2011) found that while completing a

cartoon based ToM task, individuals at high risk of psychosis showed greater activations in regions including the TPJ in comparison to both patients with diagnosed schizophrenia and healthy controls. Furthermore, diagnosed patients showed a reduction in right TPJ activation. These authors suggest high-risk patients may be showing compensatory overactivation of mentalizing regions. However, it may be that elevated right TPJ activity is a biomarker of risk for psychosis, and hyper-activation is less apparent in manifest patients due to the effects of medication, neural atrophy or compensatory brain responses. Right TPJ hypoactivation has also been reported in unaffected siblings of people with schizophrenia (e.g. Goldschmidt et al., 2014) and it is currently not clear if this is a marker of vulnerability or resilience.

Perhaps the multisensory functions of the right TPJ could further explain the symptom profile of schizophrenia. Reported perceptual dysfunctions include brighter colours, sharper sense of touch or unreality (e.g. Cutting & Dunne, 1989; and see Javitt & Freedman, 2015). Distortion of multisensory integration could further lead to abnormal feelings about body-ownership and dissociative experiences, including 'strange ghostly feelings' as if from another planet or feelings of not really existing (Sedman, 1970). Indeed, sensory features characteristic to schizophrenia can be modulated via neural stimulation of the TPJ (e.g. Blanke et al., 2002; Hoffman et al., 2005; Vercammen et al., 2009). Spence et al. (1997) reported that passivity symptoms were associated with stronger activation of the right TPJ, inferior parietal lobe and cingulate in these patients compared to other patients with schizophrenia without passivity and healthy controls. Symptom reduction was associated with a decrease in the activation level. More recently, Arzy et al. (2007) found that right TPJ activation duration was positively associated with perceptual aberration scores (based on experiencing schizotypal body schema alterations) during an own-body processing task.

If the physical and mental aspects of the self are not well integrated, one may begin to perceive a separate entity, explaining how right TPJ dysfunction may lead to sensed presence. Overactivation in this region in schizophrenia may be linked to misperceptions and hallucinations, including loss of SoA and feelings of being watched or followed. As resting state hippocampal connectivity is correlated with activation of the TPJ, shared dysfunction of these two regions could be key in determining patients' symptoms (Wible, 2012). Specifically in relation to auditory hallucinations, Wible (2012) discusses the involvement of a large portion of the TPJ in representing audio-visual speech (e.g. Wright et al., 2003) and that hearing voices is linked to TPJ activation (Kriegstein et al., 2004). For example, abnormal functional connectivity between left TPJ and right inferior frontal gyrus may underlie auditory hallucinations (Vercammen et al., 2010). Therefore, dysfunction of neural regions involved in processing language in addition to TPJ dysfunction (i.e. problems with multisensory integration and controlling self and other representations) could underlie hearing voices. The

reported association between self/other attribution of auditory hallucinations in schizophrenia and the sulcal pattern of the right posterior sylvian fissure region (Plaze et al., 2015), imply that the morphology of right TPJ may be a particularly important factor.

3.3 Autistic Spectrum Disorder

Neurobiological models of Autistic Spectrum Disorder (ASD) emphasise the likelihood of functional disconnectivity (e.g. Frith, 2004) in addition to the importance of structures involved in social cognition. For example, one recent study reported reduced functional connectivity affecting middle temporal and superior parietal cortical areas involved in processing of facial expressions, ToM and 'sense of self' (Cheng et al., 2015). However, connectivity between the TPJ and insula may be worthy of attention given that the anterior insula is a consistent area of hypoactivation in ASD (Di Martino et al., 2009).

Social cognition and TPJ dysfunction link schizophrenia and ASD. In fact, these disorders may be diametrically opposed (Abu-Akel et al., 2015). Many papers reporting evidence of right TPJ dysfunction in ASD (e.g. Chien et al., 2015; Kana et al., 2014; Pantelis et al., 2015) link such findings to deficits in social cognition. For example, Lombardo et al. (2011) reported that when compared to healthy controls, people with ASD showed less selective responding of the right TPJ for reasoning about mental states versus physical states, perhaps reflecting delayed neural maturation (Lombardo et al., 2011). Interestingly, other regions commonly activated by ToM tasks (e.g. ventromedial prefrontal cortex, posterior cingulate, left TPJ) were not differently activated between the groups (Lombardo et al., 2011). Other studies have reported reduced activation of TPJ when processing intentional causality when patients with ASD are compared to healthy controls (Murdaugh et al., 2014)

Cygan et al. (2014) provided event-related potential evidence for self-other blending in ASD. These individuals showed fewer neural activation differences than controls when attending to self- versus other-related information. That is, the self-preference effect was absent in ASD when the self was being compared to a close other (but this was not the case for a distant unrelated person). Children with autism are impaired at reasoning about both their own and others' mental states (Williams, 2010), including their own false beliefs (Williams & Happe, 2009). Difficulties disentangling the mental aspects of self and other could therefore lead to problems with understanding one's own mental state as well as that of other people. This would also help explain why when Kirby and colleagues explored the perceptions of children with ASD using interviews about sensory experiences, these children

showed a tendency to state that their behaviours were similar to those of other people (Kirby et al., 2015).

Williams et al. (2006) investigated the neural correlates of imitation in children with ASD. They report prominent differences in activation of the right TPJ, such that this region was active in controls during imitation but not observation, whereas the reverse pattern was apparent in ASD. Evidence of imitation behaviours such as echophenomena in ASD may signal the dysfunction of physical self-other representations, and perhaps the preferential application of more basic or rudimentary forms of social cognition based on mirroring and matching emotional and or physical states. In relation to interpersonal reactivity, ASD (like both schizophrenia and TS), has been associated with elevated personal distress in interpersonal situations despite reduced cognitive perspective taking (Rogers et al., 2007). There appears to be a reciprocal relationship between imitation and emotion contagion versus higher forms of perspective taking in relation to the right TPJ (e.g. Spengler et al., 2010), which could explain why these patients lack more complex forms of perspective taking that contribute to a more sophisticated understanding of abstract mental states. While empathy ratings in ASD can vary (e.g. Cascio et al., 2012), they have been related to white matter integrity (from the corpus callosum into the superior longitudinal fasciculus) as indicated by fractional anisotropy of the right TPJ (Mueller et al., 2013).

Pantelis et al. (2015) scanned adults with ASD while they watched a TV clip involving social comedy, revealing less right TPJ activity while viewing socially awkward situations in these individuals than controls. However, it is not clear whether the activations were linked to poorer visual attention or gaze patterns during the video-clips rather than more specific problems with ToM. Indeed, TPJ dysfunction in ASD participants could mean that these individuals are less automatically attuned to environmental cues which prompt the attribution of awareness and mental states (Castelli et al., 2002), and in turn social interaction. The theory of TPJ function proposed by Kelly et al. (2014) which combines both an attention and a self-other distinction approach could also be applied to the symptomatology of ASD.

Dysfunction of the TPJ in ASD could further explain some of patients' multisensory problems. These include multisensory integration difficulties (Foxy et al., 2015) and enhanced awareness of sensory stimuli (Kirby et al., 2015). For example, Stevenson et al. (2014) reported diminished multisensory integration in ASD based on poor perception of a visual illusion, which required perceptual fusion between vision and audition. This was interpreted by the authors to reflect poor cross-modal binding. Another study (Donohue et al., 2012) showed that whereas healthy controls experience visual and auditory stimuli as simultaneous if the visual stimulus appears slightly earlier, people with more ASD traits require the auditory stimulus to occur slightly earlier, suggesting there is a bias towards auditory information in ASD. It has also been suggested that people with ASD have a larger

temporal window of integration, which may lead to excessive binding between unrelated stimuli (Foss-Feig et al., 2010). In addition, reduced intentional binding may be seen in these patients (Sperduti et al., 2014), perhaps affecting SoA (Zalla & Sperduti, 2015). Indeed, linking mental states with physical actions could be impaired in these patients. Neuroimaging during a ToM picture task involving attribution of intentional causality revealed weaker functional connectivity between the TPJ and motor areas in ASD participants versus healthy controls (Kana et al., 2014). Furthermore, one recent study reported that right dorsal TPJ showed less connectivity with left cerebellar lobule Crus II in ASD, which may contribute to multimodal integration deficits (Igelström et al., 2016). In summary, these studies provide further evidence for a disconnection between motor, perceptual and mentalizing systems in this disorder, with a crucial role for underlying TPJ dysfunction.

3.4 Obsessive Compulsive Disorder

A number of studies have implicated brain structures such as the putamen, ventromedial prefrontal and limbic regions in OCD, highlighting a shift from goal directed to habitual behaviours (Banca et al., 2015) and alterations in reward-based learning (e.g. Hou et al., 2014; Mataix-Cols et al., 2003). More recently, however, temporal lobe atrophy has been reported in those patients with egodystonic obsessive thoughts linked to religion, morality, sex or aggression (Subira et al., 2013). Of further interest, are the results of imaging studies which indicate evidence of increased grey matter in right supramarginal and inferior parietal gyri in patients with OCD compared to healthy controls (Tan et al., 2013). In addition, patients with OCD can exhibit increased radial (but not axial) diffusivity in the TPJ (Fan et al., 2012) and hypoactivation of TPJ during cognitive tasks such as the Stroop (Page et al., 2009). It has been suggested that TPJ related P300 differences between these patients and controls could indicate enhanced attention or cognitive processes (Mavrogiorgo et al., 2002; Gohle et al., 2008).

A few studies have reported evidence of sensory distortions in OCD which could implicate the TPJ, such as poor performance on graphesthesia tests (Tumkaya et al., 2012). One recent study suggested that abnormalities in sensorimotor integration may contribute to compulsions like repeated checking (Russo et al., 2014), through self-doubt over the completion of an action due to distorted sensory feedback, which could threaten the physical aspect of the self. Furthermore, another symptom often reported in OCD that may involve distortions of multisensory integration is sensory intolerance (e.g. Hazen et al., 2008; and TS: Belluscio et al., 2011). For example, patients report oral and tactile hypersensitivity in childhood which is linked to the development of rituals (Dar et al., 2012). The possibility that

these characteristics may reflect poor multisensory integration within the TPJ is strengthened by the finding of structural abnormalities in this region (Tan et al., 2013).

Sensory incongruence may contribute to 'not just right' experiences (Leckman et al., 1994; Neal and Cavanna, 2013), uncomfortable feelings due to a strong need to achieve congruency with a particular physiological or cognitive state. These experiences are common in TS as well as OCD (Leckman et al., 1994). Feelings of 'not just right' are similar to those of incompleteness and could imply a weakened sense of physical self or poor integration between intentions, actions and sensory feedback relating to the physical and mental aspects of the self. Gentsch et al. (2012) used EEG to investigate SoA in patients with OCD and found evidence that these individuals fail to predict and suppress the sensory consequences of their own actions. These authors therefore speculate that an experience of mismatch between expected and actual sensory outcomes could lead to the feelings of incompleteness in these patients and repetitive behaviours aimed at reducing this sense of incompleteness. This impaired sensory matching may reflect TPJ dysfunction. In fact, similar dysfunctions affecting SoA could contribute to perceptions of involuntary movement in conversion disorders (see Voon et al., 2010). In such cases, perceiving a mismatch between intentions and actions, or anticipated and actual sensory feedback make lead to movements being perceived as involuntary. Elucidation of the neural mechanisms underlying SoA is of great importance given its likely relationship with a range of problematic impulsive and compulsive behaviours.

Only a few studies have investigated social cognition in relation to OCD, and those reporting differences between these patients and controls tend to link impairment to memory demands (Sayin et al., 2010) or symptoms associated with psychosis (Ntouros et al., 2014; Whitton & Henry, 2013). However, it has been suggested that people with OCD may be more consciously aware of their own thoughts than people with auditory hallucinations (Garcia-Montes et al., 2006), perhaps reflecting a stronger sense of mental self. Garcia-Montes et al. (2006) compared the metacognitions of patients with the symptoms of either OCD or psychosis and controls. Both current hallucinators and people with OCD were more likely to have negative beliefs about how that their thoughts could have a direct impact on the external world (e.g. 'thought action fusion'). Perhaps these perceptions could stem from an imbalance in the strength or integrity of the mental and physical aspects of the self? A stronger sense of mental self may lead these patients to associate their thoughts or intentions more directly with external events. That is, while people with normal multisensory functions can rely on physical cues to know they have performed an action, OCD patients may rely less on these judgments, based previous experience of poor multisensory convergence (e.g. Gentsch et al, 2012). Thought-action fusion or magical thoughts (e.g. thinking negative thoughts will make bad things happen) could therefore reflect a

combination of hyper-mentalizing (i.e. increased salience of one's mental states or intention) in combination with loss of physical SoA due to multisensory dysfunction. It could be speculated that patients' compulsions reflect attempts to make stronger links between the mental and physical aspects of the self (or SoA) and avoid disintegration of the self-representation or faulty other-attributions.

4. Concluding remarks

The TPJ appears to underpin functions that contribute to our sensory experiences of the material world (physical aspects of the self), and/or our appreciation of internal mental and motivational states (mental aspects of the self). A failure of processes that underpin the physical, or mental aspects of the self, may lead to faulty other-attributions. In addition, perhaps problems integrating the mental and physical aspects of the self, could lead the overall sense of self (i.e. perception of being an individual entity acting at will within an external world) to break down.

In neuropsychiatric disorders like OCD, ASD schizophrenia and TS, deficits in multisensory integration and social cognition may compromise the self-representation. More specifically, reduced SoA and impulsivity may develop where the physical and mental self are not perceived to be integrated, while compulsive behaviours may represent attempts to link the mental and physical components of the self. In OCD, emotions and motivations are salient for both self and other, but defects in multisensory integration may encourage compulsive rituals which serve to restore a sense of personal agency and in turn the sense of self. Perhaps in ASD, self-other blending leads to problems with social cognition, and difficulties in allocating attention across the physical and mental aspects of the self and other. In schizophrenia, both the physical and mental aspects of self can be significantly threatened, leading to a greater loss of agency and an aversion to perspective taking. TS may comprise more threat to the self-representation than OCD, but in these patients, a strong self-localised multisensory component may drive tics which provide a source of sensory feedback that in turn help maintain a physical sense of self and agency. Similar arguments may be applied to functional disorders (Table 1).

Future studies are urged which will test these hypotheses. In particular, few studies have investigated SoA in either OCD or ASD. Likewise, studies investigating self-other differentiation are merited in patients with functional disorders. It may be expected that patients exhibiting more evidence of particular clusters of symptoms listed in Table 1 would show impairment on measures of social cognition, agency judgment or sensory binding

tasks. Specific predictions could include impairments on tasks assessing motor-imitation inhibition (e.g. Brass et al., 2000) in psychosis, deficits on ToM and/or multisensory integration tasks in people who frequently report sensed presence, or greater deficits on SoA intentional binding tasks (e.g. Moore & Obhi, 2012) in patients who exhibit impulse control disorders.

This review reflects a right TPJ emphasis based on existing literature. However, it is important to acknowledge that the true extent of lateralisation in the function of the TPJ is still open to debate. Many studies reporting right TPJ activation also report left TPJ activations, although these may cancel out as a result of statistical contrasts or appear less prominent and therefore evoke less discussion (Geng & Vossel, 2013). Moreover, some studies have demonstrated that first-person perspective versus third-person perspective simulations (Ruby & Decety, 2001) or self versus other attributions of agency (Chaminade & Decety, 2002) lead to asymmetrical activation of the inferior parietal lobe across hemispheres (see Section 2.1). Differential activation across hemispheres is therefore an important topic for future investigation.

Awareness that TPJ dysfunction can threaten one's sense of self or impair self-other differentiation prompting the development of psychiatric symptoms highlights significant opportunities for innovative therapeutic impact. In relation to pharmacological treatments, drugs that alter norepinephrine may influence TPJ function (e.g. during attention related tasks: Strange & Dolan, 2007), whereas selective serotonin reuptake inhibitors have been reported to enhance task-related activation in this region on a social cognition task in patients with intermittent explosive disorder (Cremers et al., 2016) and on a language processing task in depression (Abdullaev et al., 2002). In addition, intranasal oxytocin was suggested to be associated with increased left TPJ activation during social cognitive tasks linked to prosocial actions (Hu et al., 2016). More generally, it has also been reported that mindfulness based therapy may also be linked to grey matter alterations in the TPJ (Holzel et al., 2011). Perhaps the most persuasive evidence suggests that TMS and tDCS can be applied to influence TPJ function (Donaldson et al., 2015). It is not yet clear whether disruption to self and other representations may occur in association with atypical structural or functional neurodevelopment involving the right TPJ, such as reduced neural pruning in childhood or functional connectivity abnormalities acquired during adolescence. Whatever the case, studies should investigate whether cortical stimulation could assist with a range of symptoms thought to reflect TPJ dysfunction (Table 1.). There is no doubt that continued exploration of the TPJ will have much to offer scholars across the realms of neuropsychology, neuropsychiatry and philosophy of mind.

Table 1. Neuropsychiatric symptoms hypothesised to reflect temporo-parietal dysfunction

Disorder	Symptom	Disrupted function	Hypothesised effect
Schizophrenia	Paranoia, delusions of reference, anthropomorphism	Theory of Mind	Excessive
	Reduced perspective taking, ToM deficits	Theory of Mind	Inadequate
	Imitation, elevated personal distress	Self-other blending	Excessive
	Magical thinking, grandiosity, delusions of reference	Personal sense of agency	Excessive
	Delusions of control, auditory hallucinations, impulsivity	Personal sense of agency	Inadequate
	Dissociative experiences, sensing a presence	Multisensory integration	Inadequate
Tourette syndrome	Hyper-mentalizing, anthropomorphism, socially inappropriate urges	Theory of Mind	Excessive
	Reduced perspective taking, ToM deficits	Theory of Mind	Inadequate
	Imitation, elevated personal distress	Self-other blending	Excessive
	Compulsive 'just-right' behaviours (e.g. complex tics, symmetry), premonitory urges to tic	Multisensory integration	Inadequate
	Tics, impulse control problems	Personal sense of agency	Inadequate
Obsessive compulsive disorder	Magical thinking in relation to compulsive acts	Personal sense of agency	Excessive
	Compulsive 'just-right' behaviours (e.g. ordering, arranging, checking)	Multisensory integration	Inadequate
Autistic Spectrum Disorder	ToM deficits, social withdrawal, socially inappropriate behaviours	Theory of Mind	Inadequate
	Imitation, elevated personal distress	Self-other blending	Excessive
Functional disorders	Depersonalisation	Self-other blending	Excessive
	Body dysmorphism, derealisation	Multisensory integration	Inadequate
	Dissociative symptoms, functional motor symptoms	Personal sense of agency	Inadequate

Funding

This research received no specific funding.

Acknowledgments

With thanks to Peter C. Hansen of University of Birmingham, who assisted with the creation of Figure 1. Anonymous reviewers of this paper offered many helpful comments.

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