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Agency performance modulates resting-state variation in prefrontal brain regions

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ABSTRACT

Distinguishing the effects of own from others' actions is a prerequisite for effective interpersonal functioning. Individuals differ in their ability to do this. For example, difficulties in self-other attribution have been linked to positive symptoms of schizophrenia such as hallucinations, with causally ambiguous situations proving a universal challenge. The goal of the present study was to examine relationships between individual differences in resting-state functional connectivity and self-other attribution performance. Fifty-five healthy adults completed a resting-state fMRI scan and an attribution task that involved tapping at irregular intervals while listening to a tone sequence. The likelihood that tones in the sequence corresponded to the participant's taps was systematically varied. Using group independent component analysis (ICA) and dual regression, we found that connectivity between prefrontal networks associated with self-referential processing and regions sensitive to externally-generated stimuli was modulated by participants' ability to accurately assess the proportion of tones belonging to self versus other. These findings shed additional light on the neural mechanisms of agency, emphasising that connectivity with prefrontal networks play an important role in self-other differentiation.

1. Introduction

Our waking day is filled with encounters that involve coordinating our own thoughts and behaviours with those belonging to other individuals. A prerequisite for doing this is the ability to distinguish acts of the 'self' from those of 'others' by forming accurate predictions about action-outcomes (Wolpert et al., 1995; Frith, 2005; Wegner, 2003). Even in the absence of others, we think about, and attempt to work out who is responsible for events that have or will take place. The sense of agency, the feeling that 'I am in control of my thoughts, actions and their consequences' (Gallagher, 2000) is a complex and multifaceted phenomenon that can be influenced by sensorimotor processes as well as by individuals' mental and emotional states; their intentions, expectations and biases (Synofzik et al., 2008, 2006; Dijksterhuis et al., 2008; Farrer et al., 2008; Sato, 2009; Wegner, 2003).

Evidence suggests that individuals differ in their ability to objectively distinguish between events caused by self from those caused by other individuals. Difficulties associated with this fundamental skill is thought to be a core cognitive feature of schizophrenia, reflected in positive symptoms like delusions of control and auditory verbal hallucinations (Waters et al., 2012; Ditman and Kuperberg, 2005; Frith, 2005; Jeannerod, 2009; Spence et al., 1997). Performance discrepancies have also been shown in non-clinical samples (Sugimori et al., 2011; de Bezenac et al., 2015). For example, de Bezenac et al. (2015) found that accuracy in assessing the proportion of self-other control over auditory events decreased with hallucination proneness and, as anticipated, increased with music-making experience. This pattern of results was accentuated by task difficulty, i.e., in conditions where tones were as likely to belong to self as to other. Agency performance is therefore also determined by how an individual's previous experiences and expectations and cognitive biases interact with external factors (Wegner, 2002, 2003), such as the amount of prior information available to facilitate this decision-making.

Previous neuroimaging studies into sense of agency have examined brain activity as participants performed attribution tasks in the scanner. For example, studies have compared response to unaltered visual feedback of action with feedback that has been distorted using delay (e.g., Leube et al., 2003) or spatial displacement (e.g., Farrer et al.,

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2003; David et al., 2007). These paradigms have implicated a number of disparate regions involved in sensorimotor control and multimodal integration (for reviews see Sperduti et al., 2011, David et al., 2008). Some regions, such as the insula, display particular sensitivity to clearly self-produced outcomes (e.g., Farrer et al., 2003). However, most other implicated regions have been primarily associated with action-outcome discordance typical of externally generated stimuli, though some have also shown sensitivity to self-agency (Renes et al., 2015). These include the inferior parietal lobe (Farrer et al., 2003; Chaminade and Decety, 2002), extrastriate body area (EBA) (David et al., 2007), medial and dorsolateral prefrontal cortex (Pfeifer et al., 2007; Schnell et al., 2007), and cerebellum (Blakemore et al., 1999, 2002).

Patients experiencing the positive symptoms of schizophrenia have shown over-activation of the inferior parietal lobe (primarily associated with external causes) when performing attribution tasks (Spence et al., 1997; Jardri et al., 2011; Farrer et al., 2004). However, it is not yet clear how neural differences between individuals directly relate to agency performance. Increasing evidence indicates that variation in functional brain connectivity is meaningfully associated with cognitive and behavioural differences between individuals (Bassett et al., 2009; van den Heuvel et al., 2009).

FMRI studies have examined individual differences in neural response, not only during experimental tasks, but also during so called 'resting-state' - in the absence of an explicit task. Resting-state networks (RSN) have been shown largely to correspond to regions that are coactivated during the performance of specific tasks and can provide complementary information about brain function, avoiding confounds related to completing a task (Smith et al., 2009). Emerging findings suggest that the temporal and spatial organisation of such networks have behavioural and clinical relevance (for reviews see Greicius, 2008; Zhang and Raichle, 2010) and remain relatively stable across time within individuals (Shehzad et al., 2009; Guo et al., 2012). RSN patterns in neurologically typical individuals have been associated with a number of cognitive function abilities relevant to agency, including working memory (Gordon et al., 2014; Hampson et al., 2006), attentional control (Kelly et al., 2008), and fluid reasoning (Cole et al., 2012) and theory of mind (Buckner and Carroll, 2007).

Network-based methods exploring co-activating areas have also been effective in highlighting neural differences between people with schizophrenia and matched controls (reviewed in Williamson and Allman, 2012; Karbasforoushan and Woodward, 2012). For example, severity of hallucinations and delusions were shown to correlate with aberrant functional connectivity in the default-mode network (DMN) (Rotarska-Jagiela et al., 2010), a set of brain regions associated in selfreferential processing (Greicius et al., 2003; Christoff et al., 2011) and aspects of social cognition (Mars et al., 2012) including source attribution (reviewed in Northoff et al., 2006). The relationship between networks has also been shown to be clinically significant. For example, the anti-correlation typically observed between the DMN (the medial prefrontal area in particular) and the central executive network (CEN) (Wiebking et al., 2014), has been implicated in processes of self-other discrimination and shown to be attenuated in individuals at risk for psychosis (Spaniel et al., 2015; Wotruba et al., 2013). It has been argued that such neural differences may explain observed misattributions of internally or externally generated stimuli and that resting-state variation may play an important role in determining the sense of agency (Robinson et al., 2015).

Despite a shift towards considering networks as opposed to isolated regions as the unit of analysis in elucidating neural processes (Friston, 2011; Meehan and Bressler, 2012), network accounts of agency are scarce (David et al., 2007, 2008; Robinson et al., 2015). This line of research, however, has the potential to shed additional light on the functional relationships between brain regions previously implicated in self-other differentiation and the processes leading to agency difficulties and symptoms thought to be related to this facility. The current study aims to shed additional light on self-other processing by examining the

relationship between performance on an agency task and functional connectivity in resting state fMRI.

More specifically, 55 participants completed a resting state fMRI scan and a behavioural task that involved tapping at irregular intervals while listening to a tone sequence. The likelihood that tones in the sequence corresponded to the participant's taps was systematically varied (see de Bezenac et al., 2015). Tones within the sequence that did not belong to self (other) were generated by randomising the participant's own tap intervals. We examined participants' ability to accurately assess the proportion of tones belonging to self versus other, as well as the extent to which misattribution towards self or other increased in the most challenging ambiguous conditions, where the likelihood of self and other generated tones was equal. We tested whether functional brain networks and their relationship with one another were modulated by these attribution performance measures, using and a data-driven analysis approach involving group independent component analysis (ICA), dual regression, network analysis and permutation testing in FSL (Beckmann and Smith, 2005; Beckmann et al., 2009; Filippini et al., 2009; Smith et al., 2011).

Given the limited scope of prior research on functional connectivity and agency, the current study had a number of objectives: to (1) determine whether patterns of functional connectivity are associated with individual differences in overall task performance and in ambiguityrelated misattribution; (2) examine whether such differences are associated with RSNs composed of regions previously implicated in agency tasks; and (3) investigate how individual differences in agency performance might predict alterations in either the connectivity of RSNs with other brain regions or other large-scale RSNs. Our hypothesis was that between-individual variation in functional connectivity during rest would be associated with agency performance measures and, more specifically, in the light of previous clinical evidence, that DMN nodes would be implicated. However, based on the lack of prior research in this area, our investigation was more exploratory with regard to how exactly such individual differences would be expressed.

2. Methods

2.1. Participants

The study sample initially consisted of 57 right-handed participants with a mean age of 25 years (SD = 8; range, 19–50). Participants were recruited from the student and staff population at the University of Liverpool. All participants reported normal or corrected-to-normal vision, normal hearing and somatosensory perception. No participants reported histories of mental or neurological illness. Two participants were excluded prior to statistical analysis due to incidental neurological abnormalities, leaving a final sample of 55 participants (28 females). All participants gave written informed consent as part of a protocol approved by the ethics committee of the University of Liverpool.

2.2. Imaging protocol

Within a resting-state fMRI experiment, subjects are placed into the scanner and asked to close their eyes and to think of nothing in particular without falling asleep for a duration of six minutes. After the scanning session, all participants reported that they did not fall asleep during scanning. Scans were obtained using a Trio 3.0 T (Siemens, Erlangen, Germany), whole body MRI system, equipped with an eight-channel phased array head coil. Foam padding and head restraints were used to minimise head movement during imaging. Each scan consisted of 197 contiguous EPI functional volumes (TR = 2000 ms; TE = 25 ms; flip angle = 90°, 32 slices, matrix = 64×64 ; FOV = 192 mm; acquisition voxel size = 3.5 mm3). Before preprocessing these functional data, the first eight volumes of each run were automatically removed to allow for magnetic stabilization, leaving 180 usable volumes. To facilitate co-registration and normalisation of these functional data, we also

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