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Person perception involves functional integration between the extrastriate body area and temporal pole

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ABSTRACT

The majority of human neuroscience research has focussed on understanding functional organisation within segregated patches of cortex. The ventral visual stream has been associated with the detection of physical features such as faces and body parts, whereas the theory-of-mind network has been associated with making inferences about mental states and underlying character, such as whether someone is friendly, selfish, or generous. To date, however, it is largely unknown how such distinct processing components integrate neural signals. Using functional magnetic resonance imaging and connectivity analyses, we investigated the contribution of functional integration to social perception. During scanning, participants observed bodies that had previously been associated with trait-based or neutral information. Additionally, we independently localised the body perception and theory-of-mind networks. We demonstrate that when observing someone who cues the recall of stored social knowledge compared to non-social knowledge, a node in the ventral visual stream (extrastriate body area) shows greater coupling with part of the theory-of-mind network (temporal pole). These results show that functional connections provide an interface between perceptual and inferential processing components, thus providing neurobiological evidence that supports the view that understanding the visual environment involves interplay between conceptual knowledge and perceptual processing.

1. Introduction

Segregation and integration are cornerstones of brain organisation (Sporns, 2013). The majority of human neuroimaging research has focussed on functional segregation by identifying distinct patches of cortex with particular functional properties (Fox and Friston, 2012). For example, in the domain of social perception, anatomically and functionally distinct neural circuits have been associated with recognising and making inferences about others, respectively (van Overwalle, 2009; Kanwisher, 2010). Little is currently known, however, regarding how signals from such distributed neural circuits are integrated (Kanwisher, 2010; Sporns, 2014). The current fMRI experiment investigates the contribution of functional integration to social perception.

Over the last 20 years, evidence has supported the view that segregated neural circuits underpin distinct social processes (Adolphs, 2009). The detection and recognition of other human agents on the basis of their physical features (body perception) engages patches of cortex along the ventral visual stream, including occipito-temporal cortices and fusiform gyri (Kanwisher, 2010). In addition, person knowledge research has identified a brain network that is engaged when representing others' mental states, such as beliefs, desires, and attitudes, which is known as the Theory of Mind (ToM) network (Frith and Frith, 1999; Saxe and Kanwisher, 2003; Mitchell, 2009; van Overwalle et al., 2009). The ToM-network comprises temporoparietal junction (TPJ), medial prefrontal cortex (mPFC), temporal poles, and precuneus, and has been shown to be active when inferring traits, such as whether someone is helpful or selfish (Ma et al., 2011). Together, both body perception and ToM processes have been argued to form a network that contributes to understanding who someone is and how we might expect them to behave (Haxby et al., 2000).

Within a network model framework, body perception and ToM networks can be considered as distinct processing components, which are linked together by anatomical and functional connections (Meunier et al., 2010; Park and Friston, 2013; Sporns, 2013). Each component in a network would perform functionally distinct processes with connections serving to integrate signals across components (Sporns, 2014). Although network models of brain function are supported by research in comparative, theoretical and systems biology (Meunier et al., 2010; Sporns, 2010; Bassett and Gazzaniga, 2011; Wig et al., 2011), empirical evidence demonstrating how and when neural circuits communicate is

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limited. Indeed, by measuring the magnitude of regional brain responses the ventral visual stream and ToM networks have been associated with linking together physical features of a person with social knowledge (Todorov et al., 2007; Vrtička et al., 2009; Bayliss et al., 2012). However, the extent to which these distinct neural networks communicate during body perception remains largely unknown.

To date, one prior neuroimaging study has shown that body perception and ToM networks interact with each other when associating trait-based information with a person's body shape and posture (Greven et al., 2016). Greven and colleagues (2016) paired bodies or names with trait-based or neutral statements and asked participants to form an impression of each person. The results showed that body perception and ToM networks interact when linking physical features to personality characteristics and that this effect was tied to processing bodies more than names. More specifically, right fusiform body area (FBA) showed more coupling with bilateral temporal poles and left TPJ, while left temporal pole showed more coupling with left FBA, for traits than neutral statements and for bodies more than names. Thus, during an initial acquaintance, linking trait inferences with physical features involves integration between nodes within the body perception and ToM networks. The temporal poles have previously been implicated with binding complex information from different modalities together (Olson et al., 2007, 2013), as well as retrieving social knowledge (Simmons and Martin, 2009; Simmons et al., 2010; Drane et al., 2013). Therefore, Greven and colleagues' (2016) findings enhance functional understanding of the temporal poles by showing how they operate in partnership with the body perception network to integrate distinct pieces of social information such as body shape and trait information.

Social interactions, however, are not only guided by information received online; we frequently have stored knowledge regarding our interaction partners (Todorov et al., 2007; Vrtička et al., 2009; Cloutier et al., 2011). It is important to study recall of social knowledge because physical features not only cue identity judgments (Haxby et al., 2000; Or and Wilson, 2010; O'Toole et al., 2011), but also trait inferences that also guide social behaviour (e.g., helpful, selfish; Uleman et al., 2008; Sugiura, 2014). Prior neuroimaging work has investigated recall of social knowledge during face perception (Todorov et al., 2007; Vrtička et al., 2009; Bayliss et al., 2012), but this work did not assess functional connectivity between neural networks and instead measured the magnitude of responses. These studies showed that areas within face perception and ToM networks are involved when observing faces about which behaviours had been remembered compared to novel faces (Todorov et al., 2007), or when recognising faces that previously appeared hostile compared to friendly faces (Vrtička et al., 2009). To date, therefore, it has yet to be explored how functional connectivity between representations of physical features (face or body perception) and trait-inferences contribute to the recall of trait information during person perception.

The current fMRI study uses functional connectivity analyses to investigate the hypothesis that recall of social knowledge during person perception involves the exchange and integration of signals between the ventral visual stream and the ToM-network. Based on prior studies, we expect the temporal poles to be a key candidate for storing social knowledge (for reviews, see Olson et al., 2007; Patterson et al., 2007; Perrodin et al., 2015). In addition, we will be able to test the extent to which recall of social knowledge engages similar neural network integration as previously shown during the association of social knowledge to body shape and posture (Greven et al., 2016). For a similar pattern of results to Greven and colleagues (2016), we should expect links between the temporal poles and FBA when recalling social over non-social information.

2. Materials and methods

2.1. Participants

Twenty-four participants (15 females; mean ± SD age: 22.6 ± 4.7 years) were recruited from the Bangor community and received a monetary reimbursement of £15 for completing the fMRI experiment. All participants had normal or corrected-to-normal vision and reported no history of neurological damage. They gave informed consent according to the local ethics guidelines. For 3 participants, 2 sessions from the main task had to be removed due to excessive head motion (displacement above 3 mm). Due to a technical error during post-scanning behavioural data collection one participant's data was not recorded and therefore the post-scanning behavioural data is based on a sample of twenty-three participants (14 females; mean ± SD age: 22.6 ± 4.8 years). Stimuli were selected and validated for the fMRI experiment in a behavioural pilot experiment. The behavioural pilot experiment involved 73 participants (55 females; mean ± SD age: 20 ± 2.9 years). No participants completed both pilot and fMRI experiments.

2.2. Experimental design overview

The full experimental design comprised a 3 (Social knowledge: Positive, Negative, Neutral) x 2 (Group bias: in-group, out-group) factorial design. In order to study the recall of social knowledge, the current study collapsed the design across Group bias. All analyses in the current experiment, therefore, focus on recall of trait-based information (Positive and Negative combined) compared to neutral information (Neutral) irrespective of group bias. Analyses investigating the effect of group bias will be reported elsewhere (Greven & Ramsey, under review).

The task and stimuli were first piloted for validation purposes, in order to establish that participants could encode social information with specific bodies and later accurately recall that knowledge when prompted. Subsequently, the fMRI experiment consisted of several stages (Fig. 1): 1) Encoding phase – participants were asked to form an impression about unique body-statement pairs; 2) fMRI experiment – participants were shown each body again and asked to form an impression of them based on what they had previously learnt; 3) Recognition phase – participants had to judge which of the two bodies presented in each trial was previously paired with the shown statement. Details of each stage of the experiment and the tasks employed are provided below.

2.3. Stimuli

Pictures of bodies were adapted from Greven et al. (2016) that had been selected to convey an emotionally-neutral posture (i.e., crossed-arms or slouching postures were not included) but varied in terms of body shape, skin colour and clothing. Consistent with prior work (Downing et al., 2007), in order to target regions selective for images of bodies and not faces, images had been cropped so the head was not visible. For the pre-scanning experiment, a total of 144 bodies (72 female) were used. Two versions of each body were created using GIMP 2.8 software (www.gimp.org), one with a blue shirt and one with a yellow shirt. Blue and yellow clothing was required for analyses of group bias, but are not the focus of the current study. Participants would never see the same body in both a yellow and a blue shirt. Instead, half the participants would see bodies 1 – 72 in blue and 73 – 144 in yellow, and the other participants would see the opposite combination. Each body was only shown once during the encoding experiment, to avoid any possible effects of combining the same person with different social knowledge statements over the course of the experiment.