



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 \pm SD age: 22.6 \pm 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 \pm SD age: 22.6 \pm 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 \pm SD age: 20 \pm 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) \times 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.

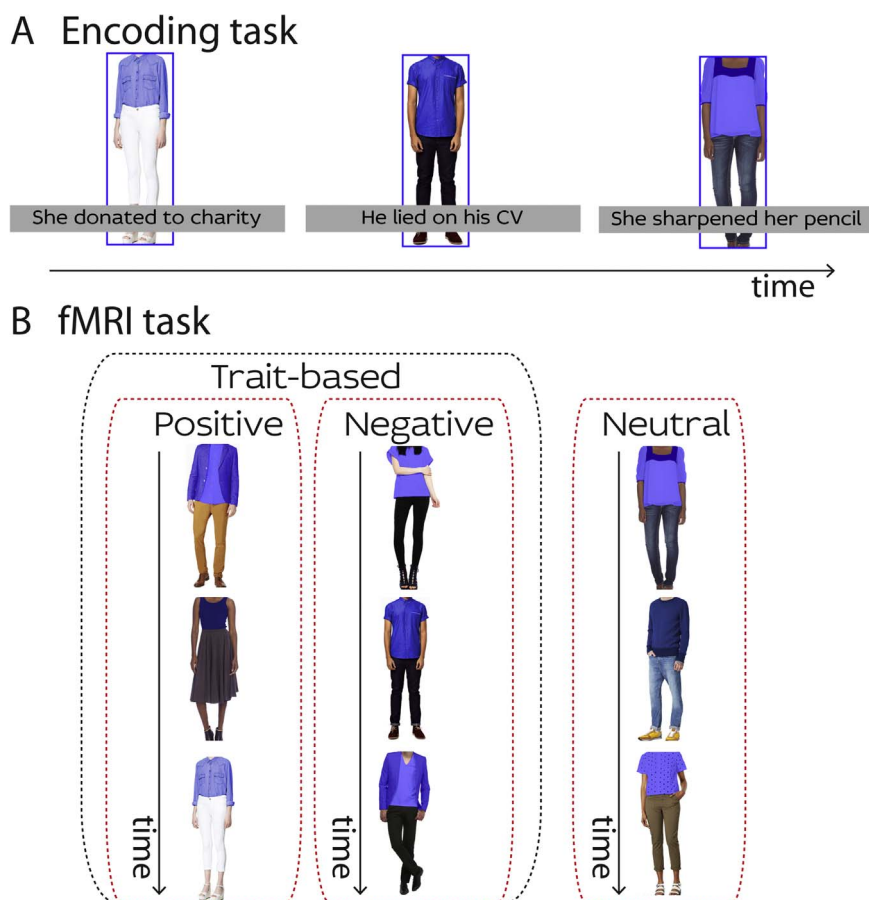


Fig. 1. Methods and procedure for the fMRI experiment. A) In the encoding task, a variety of bodies were paired with statements conveying social knowledge (positive, negative, or neutral). Participants were instructed to form an impression of these people. B) In the main task of the fMRI experiment, participants observed blocks of bodies that had previously been paired with trait-based (positive or negative) or neutral statements. The bodies were presented on their own (without the statement) and participants were instructed to form an impression of each body based on what they had previously learned about them. For the univariate and psychophysiological interaction (PPI) analyses, blocks with positive and negative bodies were combined into one regressor to compare Trait-based to Neutral bodies.

Social knowledge stimuli comprised 144 statements that were adapted from Mitchell et al. (2006) to convey either trait-based (positive and negative) or neutral information. An example of a trait-implicating statement is “He cut in front of the man in line”, implying the person is inconsiderate, whereas a neutral example is “She walked through the swivel doors”. Each statement (48 Positive, 48 Negative, 48 Neutral) was presented once during the experiment.

2.4. Behavioural tasks

2.4.1. Encoding phase

Participants were assigned to one of two different groups (Blue or Yellow) and wore a t-shirt of that colour for the remainder of the experiment. This t-shirt manipulation was part of the group bias investigation. Participants were told that they would see lots of different bodies about whom they would learn something, and later on they would be asked a number of questions about the bodies. In each trial, participants were presented concurrently with a picture of a body wearing a blue or yellow t-shirt and a social knowledge statement (Positive, Negative or Neutral). For each participant, bodies were randomly assigned to the statements. Thus, there was no systematic relationship between particular bodies and statements across participants, which removes any coupling between low-level stimulus artefacts and any one condition in our design.

The body (full-colour picture, 300×750 pixels) was presented in the middle of the screen with text (fontsize 30 pt) underneath (250 pixels below the centre of the screen). Each trial started with the presentation of a fixation cross for 500 ms, followed by the simultaneous presenta-

tion of an agent and a statement for 5000 ms. Participants were instructed to pay attention to both the person as well as to the knowledge that they would receive about that person (Traits or Neutral).

There were 144 trials in the encoding phase (48 per condition; Positive, Negative, and Neutral). Trials were presented in 8 blocks containing a random sequence of 18 trials from 3 valence conditions. Blocks alternated between a presentation of team yellow and team blue. To make sure participants paid attention to all aspects of the stimuli, at the end of each block they were asked a yes/no-question about the previous trial. Within a maximum duration of 5 s, yes/no responses were made by pressing the ‘F’ and ‘J’ button, respectively. These questions could be about the agent’s gender (was this person a man/woman?), or body (was this person facing forward?), as well as the person knowledge statements (did this person touch an object? did this person have a positive/negative attitude?). To ensure that participants remained alert to all elements of these stimuli, the content of questions could not be predicted.

2.4.2. fMRI scanning

Shortly after finishing the encoding phase (approximately 5 min), participants entered the scanner. Here, all the bodies were presented again. Participants were instructed to form an impression of these people based on what they previously learned about them. More details on fMRI scanning procedures are given below.

2.4.3. Recognition phase

After completing all tasks in the scanner, participants performed a

recognition task where all the bodies and statements were presented again. In each trial, two bodies appeared on the screen (both of the same team and gender) and a statement was shown underneath the bodies. On all trials, one of the two bodies had been previously paired with that specific statement during the encoding phase. Therefore, on every trial one body correctly matched the statement and one did not. Across trials the pairing of bodies varied such that either both bodies were previously paired with a trait-based statement (positive or negative) or both bodies were paired with a neutral statement, or one body was previously paired with a trait and the other body with a neutral statement. During this task, each body was presented twice, once as the body that had been paired with the statement and once as the body that had been paired with a different statement. There were two conditions: Traits and Neutral. For Traits, the correct answer was a body that was previously paired with a trait. On neutral trials, the correct answer was a body that was previously paired with neutral information.

2.5. Behavioural data analysis

A trial was considered an outlier if the reaction time was below 200 ms, ensuring that participants had taken enough time to read the statement and observe the bodies. This resulted in no rejected trials in the pilot experiment, and .94% of trials rejected in data collection after scanning. Participants' recognition performance (percentage accurate) was compared against chance performance (50%) for Traits and Neutral conditions, as well as across the two conditions. To do so, mean differences and 95% confidence intervals (CIs) were calculated for each condition compared to 50% as well as compared to each other. In addition, Cohen's d_z was calculated as a standardised effect size by dividing the mean difference by the standard deviation of the difference (Cohen, 1992; Lakens, 2013; Cumming, 2014).

2.5.1. fMRI experiment

During scanning, three tasks were completed (the main experimental task, a body-localiser and a ToM localiser). Details for each individual task are provided below.

2.5.2. Main experimental task

The main task used a block-design with blocks of bodies presented for 16 s. Each image (300×650 pixels) was presented for 1800 ms, followed by a blank screen for 200 ms, resulting in a total of 8 bodies per block. The same bodies presented in the encoding task were now presented during scanning and grouped together in a block according to their assigned social knowledge (positive, negative, and neutral). For example, in a 'positive' block, all 8 bodies were previously associated with positive social information. Participants were given the instruction to form an impression of each body, based on the information they learned about that body during the encoding phase. At the end of each block, participants were asked a question about the previous body relating to their gender (was this person a woman/man?) or their team (was this person part of your/other team?). From trial-to-trial, the image location was slightly jittered (4 different locations that varied by 10 pixels around a central fixation dot). From the four options, the location of the image on each trial was randomly selected.

In one functional run, 20 blocks were completed and blocks were separated by a jittered rest block with an average duration of 7 s (which varied between 5 and 9 s with 500 ms steps). Each of the 20 blocks showed bodies from one condition (Positive, Negative, or Neutral). The complete set of 20 blocks were split into two sets of 10 blocks with each set of 10 blocks pseudorandomised. Indeed, to help effectively model the influence of different events on BOLD signal, block order for the first and second sequence of 10 blocks was counterbalanced so that within each sequence, each condition was preceded equally often by all conditions (Josephs and HensonHenson, 1999; Wager and NicholsNichols, 2003; Aguirre, 2007). To provide a completely ba-

lanced block "history" across conditions, each sequence began with a "starter block", which was not included in the data analysis but modelled as a covariate of no interest. Subsequently, three further blocks from each condition were presented in a counterbalanced manner. This resulted in 6 blocks of each condition (Positive, Negative, and Neutral) within one run. Each participant completed 4 functional runs of this task, with 24 Positive, 24 Negative and 24 Neutral blocks across the experiment for a total of 192 trials per condition. For all subsequent analyses, we combine Positive and Negative into a Traits condition, which therefore has $192 \times 2 = 384$ trials.

2.5.3. Functional localisers

To localise body-selective brain regions we used an established paradigm (Downing et al., 2007; <http://pages.bangor.ac.uk/~pss811/page7/page7.html>). We presented 12-sec blocks of cars and of whole bodies (without heads). A run started with a blank screen for 14 s, followed by two alternations of each condition. This was repeated a second time, and followed by a final rest period of 14 s. Each image was presented for 600 ms, followed by a blank screen for 100 ms. Twice during each block, the same image was presented two times in a row. Participants had to press a button whenever they detected this immediate repetition (1-back task). The image location was slightly jittered in the same way as in the main task. Each participant completed two runs of this task, counterbalancing the order of the stimulus presentation (Bodies or Cars).

To localise brain regions that respond to mental state reasoning, we used an established ToM-localiser (Dodell-Feder et al., 2011; <http://saxelab.mit.edu/superloc.php>). Participants read 10 short false belief stories, in which the belief characters have about the state of the world is false. Participants also read 10 false photograph stories, where a photograph, map, or sign has out-dated or misleading information. After reading each story, participants had to answer whether the subsequently presented statement is true or false. Each run started with a 12 s rest period, after which the stories and questions were presented for 14 s combined (stories: 10 s; questions: 4 s), and were separated by a 12 s rest period. The order of items and conditions is identical for each participant. In the first run, stimuli 1–5 from each condition were presented, and the remaining stimuli were presented during the second run.

2.6. Data Acquisition

The experiment was conducted on a 3 T scanner (Philips Achieva), equipped with a 32-channel SENSE-head coil. Stimuli were displayed on a MR safe BOLD screen (Cambridge Research Systems: <http://www.crsftd.com/>) behind the scanner, which participants viewed via a mirror mounted on the head-coil. T2*-weighted functional images were acquired using a gradient echo echo-planar imaging (EPI) sequence. An acquisition time of 2000 ms was used (image resolution: $3.03 \times 3.03 \times 4$ mm³, TE =30, flip angle =90°). After the functional runs were completed, a high-resolution T1-weighted structural image was acquired for each participant (voxel size =1 mm³, TE =3.8 ms, flip angle =8°, FoV =288×232×175 mm³). Four dummy scans (4×2000 ms) were routinely acquired at the start of each functional run and were excluded from analysis.

2.7. Data preprocessing and analysis

Data were preprocessed and analysed using SPM8 (Wellcome Trust Department of Cognitive Neurology, London, UK: www.fil.ion.ucl.ac.uk/spm/). Functional images were realigned, unwarped, corrected for slice timing, and normalized to the MNI template with a resolution of $3 \times 3 \times 3$ mm and spatially smoothed using an 8 mm smoothing kernel. Head motion was examined for each functional run and a run was not analysed further if displacement across the scan exceeded 3 mm.

2.7.1. Univariate model and analysis

Each condition was modelled from the onset of the first body for a duration of 16 s. A design matrix was fitted for each participant with three regressors in total: one for bodies associated with social knowledge (Traits), one for bodies associated with neutral information (Neutral), and one for the starter blocks (Starter). Positive and Negative statements were combined into one Trait regressor in order to target our primary hypothesis. There is clear justification for hypothesising a link between person perception and Theory-of-Mind networks for the Traits > Neutral contrast. Indeed, prior research has shown that reading trait-diagnostic compared to trait-neutral statements engages the ToM network (e.g., Ma et al., 2011) and images of bodies engage the body network (Downing et al., 2001). Therefore, our hypothesis follows that combining the two (traits and bodies) may involve exchange of signals between the two networks, which may be achieved through functional integration (connectivity). However, we do not have the same rationale for expecting integration between person perception and ToM networks depending on the valence of information (positive vs. negative trait statements). As such, we do not perform analyses based on valence because we do not have any hypotheses regarding the functionality of body and ToM networks according to valence of trait information.

The main effect of social knowledge (Traits > Neutral) was evaluated for each participant individually (first-level), and then for the group (second-level). This univariate analysis served two functions. As our primary research question could only be addressed by functional connectivity analyses, the first function of univariate analysis was to identify seed regions for subsequent connectivity-based analyses. The second function enabled the test of magnitude-based hypotheses regarding the role of body perception and ToM network engagement when recalling social information from bodies. That is, we will be able to test if both body and ToM networks are preferentially involved when visually processing bodies about which trait-based information could be recalled compared to neutral bodies.

For the body and ToM localiser, a design matrix was fitted for each participant with 2 regressors, one for each condition (bodies and cars; false beliefs and false photographs). Body-selective regions were revealed by contrasting bodies and cars (Bodies > Cars). The ToM-network was revealed by contrasting false beliefs with false photographs (False Beliefs > False Photographs).

2.7.2. Psychophysiological Interaction analysis

Our primary hypothesis was that recalling social information about bodies involved functional coupling between distributed neural circuits. Specifically, coupling was predicted between body-selective patches in the ventral visual stream and the ToM-network. To test this hypothesis, we used psychophysiological interaction (PPI) analysis (Friston et al., 1997). PPI enables the identification of brain regions whose activity correlates with the activity of a seed region as a function of a task. Here we used a generalized form of PPI, which allows for comparisons across the complete design space (McLaren et al., 2012). By doing so, it is possible to see whether any voxels across the brain show a correlation with activity in the seed region (the “physiological” element) as a function of the two conditions within the main task (the “psychological” element) (Fig. 2B).

Two steps were taken to define seed regions for the PPI analysis. First, based on the group-level univariate analysis, we identified any clusters of overlap between the Traits > Neutral contrast and the functional localisers (i.e., body and/or ToM localiser) at the group-level. This group-level analysis can identify clusters showing body or ToM selectivity as well as sensitivity to the main task's contrast. Second, if clusters of overlap were identified at the group-level, we identified participant-specific coordinates for regions of overlap at the single-participant level, thus allowing for inter-individual differences in peak responses.

In the case of null-results in our group-level univariate Traits > Neutral analysis, we would use functional localiser data to define seed

regions within the body and ToM networks. These seed regions will include right EBA and FBA for the body-localiser, and bilateral TPJ, bilateral temporal poles (TP), mPFC, and Precuneus for the ToM-localiser. Volumes were generated using a 6 mm sphere, which was positioned on each individual's seed-region peak. To identify seed-region peaks within localiser data, we would use results from prior studies using the identical localiser tasks to guide selection (Dodell-Feder et al., 2011; Downing & Peelen, 2011; Downing et al., 2007; Saxe and Kanwiser, 2003). PPI analyses were run for all seed regions that were identified.

PPI models for each participant included the 3 regressors from the univariate analyses as covariates of no interest, as well as 4 PPI regressors. PPI regressors included one for the Traits and one for the Neutral condition, one for the Starter blocks, and one that modelled seed region activity (Fig. 2A). The latter two regressors (starter blocks and seed region activity) are modelled as covariates of no interest.

To create the PPI regressors, the time series in the seed region was specified as the first eigenvariate, and was consequently deconvolved to estimate the underlying neural activity (Gitelman et al., 2003). Then, the deconvolved time series was multiplied by the predicted, pre-convolved time series of each of the three regressors (Traits, Neutral, and Starter). The resulting PPI for each condition in terms of predicted “neural” activity was then convolved with the canonical haemodynamic response function (HRF) and the time series of the seed region as covariates of no interest (McLaren et al., 2012; Spunt and Lieberman, 2012; Klapper et al., 2014). Then, the same contrast as in the univariate analyses (Traits > Neutral) was evaluated for each participant individually (first-level), and then for the group (second-level).

For group-level analyses, images were thresholded using a voxel-level threshold of $p < .001$, a voxel-extent (k) of 10 voxels and a family-wise error (FWE) correction for multiple comparisons ($p < .05$). Based on our hypotheses for functional connections between body perception and ToM networks, we inclusively mask the contrasts from the main task by body and ToM localisers (Bodies > Cars and False Beliefs > False Photographs thresholded at $p < .001$, $k=10$). Inclusive masking in this manner makes sure that only body-selective areas and areas involved in mentalizing are shown. For completeness, we also report results from whole-brain analyses. To localise functional responses we used the anatomy toolbox (Eickhoff et al., 2005).

3. Results

3.1. Behavioural data

3.1.1. Pilot data

Replicating prior findings (Mitchell et al., 2004; Gilron and Gutchess, 2012), results from the pilot experiment showed that approximately 8 min after encoding information, recognition performance for traits and neutral bodies was above chance-level (Traits: $M=64.60\%$, $CI_{.95}$ [61.98, 67.21], Cohen's $d_z=1.28$; Neutral: $M=60.74\%$, $CI_{.95}$ [58.48, 63.01], Cohen's $d_z=1.09$). In addition, recall of trait information was superior to neutral information (Mean difference= 3.85% , $CI_{.95}$ [1.41, 6.30], Cohen's $d_z=.36$), but there was little difference between recall of positive and negative trait knowledge with 95% confidence intervals overlapping with zero (Positive: $M=64.17\%$; Negative: $M=66.83\%$; Mean difference= -2.66% , $CI_{.95}$ [-5.71, .40], Cohen's $d_z=-.20$). These pilot data are illustrated in Supplementary Fig 1 and demonstrate that shortly after the encoding phase (approximately 8 min afterwards), participants can accurately remember information for close to 2/3 of the bodies that they were shown during the recognition phase. These results provide confidence that during scanning, which also took place shortly after the encoding phase (approximately 5 min after encoding), a majority of bodies were accurately remembered as being previously associated with social or non-social information. Further, the results provide empirical justification for collapsing positive and negative social knowledge into one

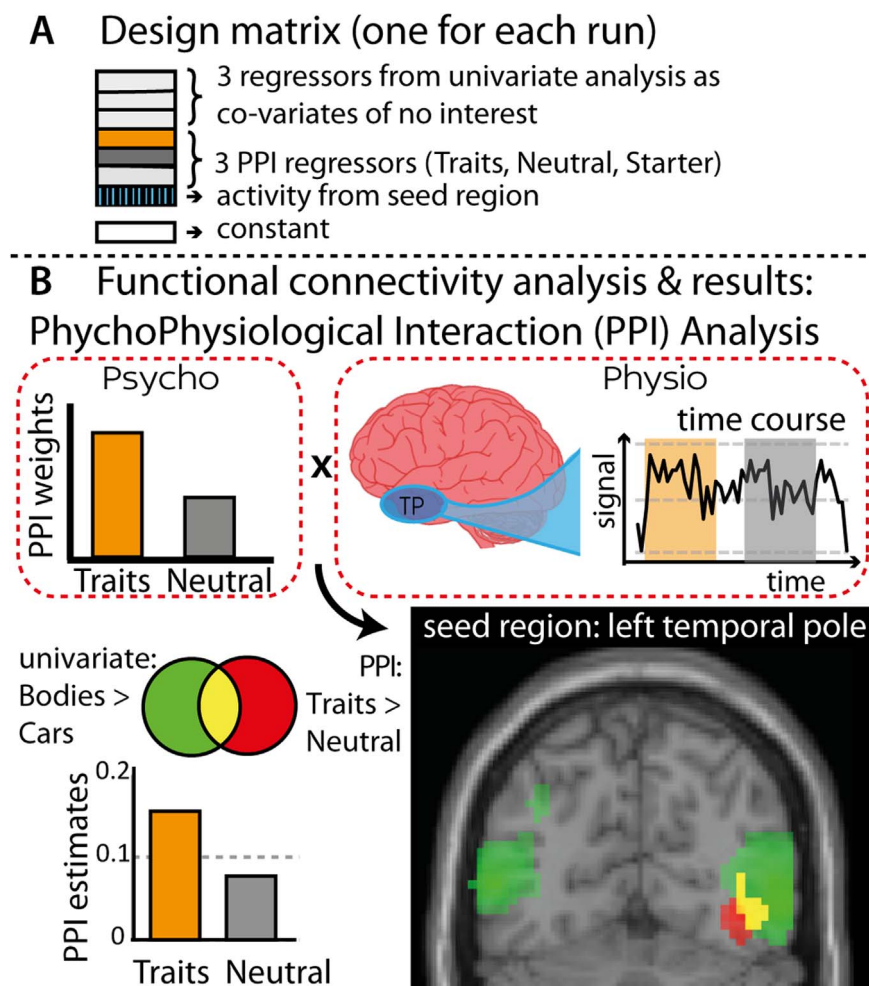


Fig. 2. PsychoPhysiological Interactions (PPI) matrix and results. A) An illustration of the design matrix (this was the same for each run), that was created for each participant. B) The “psychological” (task) and “physiological” (time course from seed region) inputs for the PPI analysis and its results. The PPI parameter estimates are extracted from a 4 mm sphere around the peak coordinate. Seed region left temporal pole showed greater functional coupling with right extrastriate body area (EBA) when recalling traits about bodies (shown in red). These areas overlapped with the body-localiser (shown in green; overlap is shown in yellow). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

‘Traits’ condition as both types of trait knowledge were recalled to a similar level.

3.1.2. Post-scanning data

After scanning, approximately 90 min after encoding, recognition performance was at chance for both trait and neutral bodies (Traits: $M=49.70\%$, $CI.95 [47.47, 51.94]$, Cohen’s $d_z=-.05$; Neutral: $M=50.97\%$, $CI.95 [48.32, 53.62]$, Cohen’s $d_z=.15$). There was also no difference between Traits and Neutral (Mean difference= -1.27% , $CI.95 [-5.30, 5.74]$, Cohen’s $d_z=.13$). Compared to the pilot data, which were collected 8 min after encoding, the post-scanning data were collected 90 min after encoding. As such, we suggest that reduced recall performance during the post-scanning recognition phase most likely reflects deterioration of recall performance over time (Supplementary Fig 1).

3.2. Neuroimaging data

3.2.1. Functional localiser analyses

Group average MNI coordinates across participants are reported in square brackets. For the Bodies > Cars contrast based on the body-localiser data, clusters were revealed in right EBA for all 24 participants [54, -70, 4], and in right FBA for 16 participants [51, -40, -23]. For the False Beliefs > False Photographs contrast based on the ToM-localiser data,

clusters were revealed in right TPJ [60, -58, 25] for 20 participants, in left TPJ [-45, -64, 28], left temporal pole [-51, 5, -32], Precuneus [-9, -49, 34], and mPFC [6, 56, 28] for 19 participants, and in right temporal pole [51, 5, -32] for 18 participants (see Supplementary Table 1 for additional details). Data across both runs of the ToM-localiser were removed for 3 participants due to excess head movement. For these three participants, the group average MNI coordinate was used to define each ToM seed region.

3.2.2. Main task univariate analyses

The Traits > Neutral contrast revealed no suprathreshold clusters when masked by either the body or the ToM localiser. Even at an uncorrected threshold, no clusters emerged within the body or ToM network.

3.2.3. Psychophysiological Interaction analyses

We hypothesised that body-selective areas would interact with parts of the ToM-network. To test this hypothesis, we used seed regions that were defined by functional localiser data.

For body-selective seed regions (right EBA and FBA), we tested for connectivity with the ToM-network that was stronger when observing bodies associated with trait-based than neutral information. No suprathreshold clusters emerged from these analyses.

ToM seed regions (bilateral temporal poles and TPJ, Precuneus, and mPFC) were hypothesised to be functionally connected with body-

Table 1.

Clusters revealed in the PsychoPhysiological Interaction (PPI) analysis for the Traits > Neutral contrast in the whole-brain analysis as well as masked by the body-localiser. Seed region is defined by the ToM-localiser (False Beliefs > False Photographs).

Region	Number of voxels	Family-wise error corrected <i>p</i> value	<i>T</i>	Montreal Neurological Institute coordinates		
				Cluster	Peak	
				x	y	z
Seed region: left temporal pole						
<i>Whole-brain analysis</i>						
Right middle occipitotemporal cortex extending into occipitoparietal cortex	177	.001	.09	5.75	39	-64 -2
			.60	4.48	30	-82 13
			.64	4.43	39	-73 -2
<i>Masked by body-localiser</i>						
Right middle occipitotemporal cortex (EBA)	44	.06	.009	5.75	39	-64 -2
			.45	3.63	45	-55 -14

Note: Regions surviving a voxel-level threshold of $p < .001$ and 10 voxels are reported. Subclusters at least 8 mm from the main peak are listed. The seed region left temporal pole met these criteria. No other seed regions from the ToM localiser showed suprathreshold clusters.

selective areas. Left temporal pole showed greater coupling with right EBA when observing bodies associated with trait-based than neutral information (Fig. 2B; Table 1). When inclusively masked by the body localiser, the response in right EBA survived FWE correction for multiple comparisons at the peak level ($p=.009$) and was at a borderline significance value at the cluster level ($p=.06$). At the whole-brain analysis level, only one cluster emerged, which had a peak in right EBA and extended into occipitoparietal cortex (Table 1). No other regions in the ToM network were coupled with body patches. To test the possibility that the result in right EBA was driven by group membership, we evaluated the social knowledge (traits vs. neutral) by group membership (in-group vs. out-group) interaction for the left temporal pole seed region. The social knowledge by group interaction [(Traits_In-group > Neutral_In-Group) > (Traits_Out-Group > Neutral_Out-Group)], as well as the inverse contrast, revealed no suprathreshold clusters when masked by either the body or the ToM localiser. Therefore, we are confident that the relationship between temporal pole and EBA is tied to the recall of social knowledge from bodies in a manner independent of group bias.

4. Discussion

The neuroscience of social cognition has largely focussed on identifying segregated neural circuits that process distinct aspects of cognition with less attention focussing on how integration between circuits contributes to perception and cognition (Adolphs, 2009). Here we show that neural networks that have previously been associated with distinct functions, such as person recognition and trait inference (van Overwalle, 2009; Kanwisher, 2010), also cooperate when social inferences are prompted by person recognition. Prior work has that associating traits with bodily features involves functional coupling between neural circuits underpinning body perception and ToM (Greven et al., 2016). The current study extends this work to show how recall of social knowledge, which is prompted by recognising bodily features, is supported by functional integration between body circuits and the ToM network. Using functional connectivity analyses, we demonstrate that a node in the ventral visual stream that selectively responds to images of bodies (right EBA) is functionally linked with a node within the ToM network (left temporal pole). The exchange of signals is specifically tied to seeing others that prompts the recall of

social knowledge: functional coupling is greater when the observed person has been associated with trait-based information (e.g., “She gave money to charity”) than with neutral information (e.g., “He put a bowl in the cupboard”). These data extend previous work by showing how integration of neural signals, rather than segregation, contributes to social perception.

4.1. Neural network integration during person perception

Greven and colleagues (2016) showed functional interplay between FBA and temporal poles when *forming* links between physical features and social knowledge, whereas the current study shows that EBA and temporal poles interact when *recalling* stored knowledge based on physical features. The temporal poles have previously been associated 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). Considered together, functional connectivity data across two fMRI studies shows evidence for interplay and partnership between temporal poles and body-selective cortex. That is, the temporal poles do not act alone during the formation and recall of social knowledge; rather, they interact with perceptual input. These findings provide neurobiological evidence in favour of the view that understanding the visual environment involves dynamic interplay between conceptual knowledge and perceptual processing (Collins and Olson, 2014a). Indeed, by measuring the magnitude of BOLD response, prior neuroimaging research has implicated body perception and ToM networks with linking together facial features and social knowledge (Todorov et al., 2007; Vrtička et al., 2009; Bayliss et al., 2012). Here, we extend the understanding of person perception by showing that a node within what is commonly considered a perceptual circuit serves to exchange signals via longer-range connections with a node in a largely inferential circuit. We suggest that longer-range connections provide an interface between perceptual and inferential processing components, which enables recall of stored social knowledge triggered by the physical features of a person.

The results from Greven and colleagues’ (2016) study as well as the current study highlight possible divisions in how nodes within social circuits are coupled during social perception. The temporal poles link differently with EBA and FBA, depending on whether traits are being associated in a novel manner (Greven et al., 2016), or recalled from memory as in the current study. It is possible that when linking physical and trait characteristics together (Greven et al., 2016), interactions between the temporal poles and FBA provide a holistic representation of the person’s identity, which is consistent with the proposed functionality of FBA (Peelen and Downing, 2005; Taylor et al., 2007; Brandman and Yovel, 2016). By contrast, when participants are asked to form impressions based on what they have associated with each body previously as in the current study, identification may take place at the earliest possible opportunity and thus not require holistic processing of identity in FBA, but instead focus more on body-part processing in EBA (Peelen and Downing, 2007; Urgesi et al., 2007; Pitcher et al., 2009). Thus, the relationship between EBA and left temporal pole would index early identification of bodily features, which trigger recall of stored social knowledge in left temporal pole. These suggestions, however, remain highly speculative and an important avenue for future research will be to test for possible functional divisions in the way the body perception and ToM networks interact with each other. For example, methods such as dynamic causal modelling (DCM), which estimate the direction of influence between regions, would be important (Friston et al., 2003; Stephan and Friston, 2010; Vossel et al., 2012). DCM relies on Bayesian statistics rather than a correlational approach, which allows the estimated evidence for different models of brain function to be compared. Using these methods, the suggestions made above regarding functional specificity and the direction of influence between person perception and ToM networks could be directly tested.

4.2. Towards a network model of social perception

Network theory is a framework in which to study organisational structure of complex systems, which is founded on understanding relations between interacting parts (Bullmore and Sporns, 2009; Meunier et al., 2010; Sporns, 2010; Bassett and Gazzaniga, 2011; Wig et al., 2011). Based on network theory, future work may aim to distinguish between signals that integrate across components from those that reflect local processing within a component (Sporns, 2013). Moreover, in many different types of network (biological, social, artificial), complex networks have common features such as ‘hubs’ and a ‘rich club’ of commonly connected circuits, and links between networks can have direction, valence and a particular weight of influence (Wig et al., 2011). Applying network theory to the study of brain organisation is a challenging prospect theoretically and empirically (Bassett and Gazzaniga, 2011), but it may hold promise for a richer understanding of social perception. For instance, if the temporal poles act as a ‘hub’ of social knowledge, which can link with different perceptual inputs (faces, bodies, voices), network theory may provide a rich foundation to empirically test this hypothesis.

4.3. Limitations and future directions

Pilot data suggest that during scanning, recall accuracy was above chance-level performance, but far from perfect (approximately 60–66% accurate). Therefore, our results are likely to underestimate the strength of relationship between the body and ToM networks since approximately 1/3 of trials may not have been remembered accurately. Unlike some studies (Todorov et al., 2007; Vrtička et al., 2009; Gilron and Gutchess, 2012), we cannot separate trials where information was recalled accurately and compare it to trials where it was inaccurate because the study was not designed to address this question. However, our best estimate is that the majority of trials in a block were remembered accurately. Therefore, any block comparisons would be biased more by correct than incorrect trials. Future work would be more sensitive to detect a wider range of effects if a greater proportion of trials could contribute to the contrast of interest.

In the current study, univariate analyses show no differences between traits and neutral information and we only find one connection between body perception and ToM networks that shows a modulation by social inference (Traits > Neutral). There are at least two ways to consider this combined pattern of univariate and connectivity results and future research will have to tease them apart by running further experiments. First, it could reflect functional specialisation. That is, recall of social knowledge prompted by body perception is primarily subserved by functional links between right EBA and left temporal pole. A weaker inference along the same lines would be that the link between right EBA and left temporal pole is the only effect that is detectable with our design but other functional connections may also support the same cognitive process. Alternatively, it could reflect a Type-1 error or false positive. The result does survive correction for multiple comparisons, which restricts the likelihood of false positives (Eklund et al., 2016), but nonetheless the result could still reflect a false positive. Future research and particularly meta-analyses will be the best way to determine the most robust estimate of the effect (Cumming, 2014).

Finally, functional connectivity analyses provide no direct insight into the underlying neural pathways that control functional coupling between brain areas. Further investigation into anatomical connections such as those linking the ventral visual stream to the anterior temporal lobes (Collins and Olson, 2014b), would complement and inform the current results. In addition, as the architecture of the neural network underpinning social perception becomes clearer, models of directional influence can be tested using appropriate analytical tools (Friston, 2009). Such future approaches would allow further development of Haxby and colleague’s model of person perception (Haxby et al., 2000)

by providing a richer understanding of the links between the many processing components of person perception.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neuropsychologia.2017.01.003.

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