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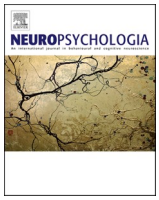

Configuration of the action observation network depends on the goals of the observer☆

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ABSTRACT

Observing the actions of others engages a core action observation network (AON) that includes the bilateral inferior frontal cortex (IFC), posterior superior temporal sulcus (pSTS) and inferior parietal lobule (IPL) (Caspers et al., 2010). Each region in the AON has functional properties that are heterogeneous and include representing the perceptual properties of action, predicting action outcomes and making inferences as to the goals of the actor. Critically, recent evidence shows that neural representations within the pSTS are sharpened when attending to the kinematics of the actor, such that the top-down guided attention reshapes underlying neural representations. In this study we evaluate how attention alters network connectivity within the AON as a system. Cues directed participant's attention to the goal, kinematics, or identity depicted in short action animations while brain responses were measured by fMRI. We identified those parcels within the AON with functional connectivity modulated by task. Results show that connectivity between the right pSTS and right IFC, and bilateral extended STS (STS+) were modulated during action observation such that connections were strengthened when the participant was attending to the action than goal. This finding is contrasted by the univariate results, which no univariate modulations in these brain regions except for right IFC. Using the functional networks defined by Yeo et al. (2011), we identified the parcels that are modulated by the attention to consist mainly of the fronto-parietal control network and default mode networks. These results are consistent with models of top-down feedback from executive system in the IFC to pSTS and implicates a right lateralized dual pathway model for action observation when focused on whole-body kinematics.

1. Introduction

The action observation network (AON) is a large-scale brain network that supports the perceptual encoding and recognition of actions performed by others (Molenberghs et al., 2012). Classically characterized as a frontoparietal system specialized for understanding goal-directed hand actions (Rizzolatti and Matelli, 2003), the complete AON more broadly supports our ability to represent many types of actions, to predict the likely outcome of goal-directed actions, and to make inferences as to the goals of others as derived through that individual's body movements (Thompson et al., 2019).

Despite the long history implicating the action observation network in action understanding, the nature of information and connectivity structure within the system is not yet fully clear. When observing actions, there are multiple levels of abstraction at which the events can be represented, from the perceived kinematics to predicted outcomes of the actions or the hidden intentional state of the observer (Bach and Schenke, 2017; Thompson et al., 2019). Each of these is linked to distinct nodes within the AON. For example, empirical studies find evidence for mid-level representations in the left anterior intraparietal sulcus (aIPS) and inferior frontal cortex (IFC), such as the identification of unique action goals (Hamilton and Grafton, 2008), predicting the likely outcomes of actions (Koul et al., 2018; Möttönen et al., 2016), and representing violations of anticipated outcomes (de Lange et al., 2008; Shultz et al., 2011). In contrast, the posterior superior temporal sulcus (pSTS) is proposed to host lower-level representations that are more

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perceptually grounded (Masson and Isik, 2021; Pavlova, 2012; Pitcher and Ungerleider, 2021). The pSTS has neural signals that differentiate different action categories (Kable and Chatterjee, 2006), is viewpoint invariant (Grossman et al., 2010) and has activation patterns that are qualitatively modulated by the goals of the observer (Tavares et al., 2008). It is important to note that this distinction between abstracted and perceptual representations is not fully dichotomous, as previous studies have also proposed the pSTS to also contribute to representing the hidden states of others (Grèzes et al., 2004; Pelphrey et al., 2004; Schultz et al., 2004; Osaka et al., 2012).

Given the many possible levels at which actions can be interpreted, an important consideration in characterizing the AON includes the cognitive demands of the task (Kemmerer, 2021; Bach and Schenke, 2017; Vallacher and Wegner, 1987). Evaluating an action with the focus on how it is being achieved (the kinematics or implementation) versus why that action is being performed (the intent) alters patterns of brain activation in the AON and lateral temporal cortex (Spunt et al., 2010, 2016). Whereas evaluating how an action may be implemented more strongly activates premotor (PMC), posterior parietal cortex and the left posterior middle temporal gyrus (pMTG), evaluating intent engages a more right lateralized system (Van Overwalle and Baetens, 2009). Moreover, when observers make a deliberate cognitive shift in the level of abstraction (i.e. from the more concrete how towards the more abstract why), this shift in cognitive representation is reflected in the BOLD amplitude of the bilateral anterior STS (Spunt et al., 2016). Even shifting focus from the more social and intentional aspects of an action to the spatial properties of the event alters the patterns of activation along the STS (Tavares et al., 2008). These findings highlight the importance of cognitive context in action understanding and extend the AON to include brain systems supporting conceptual and semantic cognitive processes and form the basis for a proposed lateral stream in action understanding (Wurm and Caramazza, 2021; Pitcher and Ungerleider, 2021).

Therefore one goal of this study is to characterize functional connectivity within the AON during action observation, and evaluate how connectivity changes in conjunction with the goals of the observer. In a previous study using multivariate pattern decoding we found that whole-body actions were decoded more accurately in the right pSTS when attending to body kinematics (how an action is achieved) versus the actor's identity (who is performing the action) or the goals (where are the target objects) (Stehr et al., 2021). Under those same attentional conditions, connectivity was strengthened between the right pSTS and the right inferior frontal cortex (IFC). We interpreted these findings as evidence for a sharpening of perceptual representations in sensory cortex mediated by top-down signals derived from internal models constructed in prefrontal cortex (Geng and Vossel, 2013; Sokolov et al., 2018; Patel et al., 2019; Kilner and Frith, 2007). The current study seeks to identify at a more granular level those regions within the IFC and also AON, including extended connected regions of the lateral temporal lobe that are modulated by shifting attention between the kinematics (the "how") or goals (the "why) during action recognition (Spunt et al., 2010).

A secondary goal of this study is to more carefully characterize the functional systems modulated by top-down goals of the participant during action observation. The IFC is a functionally heterogeneous region, with a gradient of specialization throughout as revealed through a meta-analysis across task domains (Hartwigsen et al., 2018). While the more dorsal and anterior aspects of the IFC are more strongly engaged during cognitive tasks, posterior aspects are more closely related to somatomotor networks, and ventral aspects are more closely driven by social cognitive and emotional processing. With specific regards to action recognition, evidence shows the more concrete aspects of actions (ie. how an action is achieved as conveyed through body kinematics) are represented on the more posterior IFC, whereas action goals (why an action is being executed) are associated with the more anterior extent (Kilner, 2011). Likewise, posterior parietal cortex has distinct hubs within which concrete somatomotor representations are different from the semantic and executive systems (Numssen et al., 2021). Gradients of abstraction in the AON may reflect distinct targets of information pathways specialized for online visuomotor representations of actions versus the more durable ventral conceptual pathway (Rizzolatti and Matelli, 2003; Buxbaum and Kalénine, 2010b; Binkofski and Buxbaum, 2013; Wurm and Caramazza, 2021).

Moreover, a large-scale effort is underway to reduce the complexity of brain networks to a small set of core functional networks that account for a significant proportion of the variance in brain states, as assessed in the resting state and often applied as network labels during task-related fMRI (Yeo et al., 2011; Schaefer et al., 2018; Kong et al., 2021). Using this approach, previous studies have identified dominant functional systems and topographic organizations within the inferior frontal cortex and posterior parietal lobe (Hartwigsen et al., 2018; Numssen et al., 2021). In this analysis we therefore adopt an atlas parcellation scheme that subdivides large regions of interest in the AON into small atomic parcels, assign functional networks labels to those parcels labels according to standardized functional network organization and draw inferences as to the larger functional systems that are modulated during goal-direction action observation.

2. Methods and materials

2.1. Participants

Twenty-four healthy adults (8 male, 17 female) ranging in age from 21 to 42 years old (mean = 24.7, SD = 3.6) with normal or correct-to-normal vision were recruited from the University of California Irvine campus and surrounding community. All participants gave written informed consent and all experimental procedures were approved by the University of California Irvine Institutional Review Board. One participant was excluded from the analysis due to excessive motion during scanning.

2.2. Image acquisition and preprocessing

Full details on image acquisition and preprocessing can be obtained in Stehr et al. (2021). Briefly, images were acquired on a 3 T S Prisma MRI scanner (Siemens Medical Solutions) equipped with a 32-channel receive-only phased array head coil. T1-weighted images (1 × 1x1 mm) were reconstructed into native surface-based representations using FreeSurfer's recon-all algorithm (http://surfer.nmr.mgh.harvard.edu/). Functional images were acquired with in-plane resolution = 2 × 2x2 mm (no gap) using multiband, interleaved slice acquisition. Functional scans designed to localize the pSTS were acquired with TR = 2000 ms (69 axial slices) and scans designed to capture task-related modulations in functional connectivity were acquired with TR = 1500 ms (68 axial slices). Functional images were slice-time corrected, 3D motion corrected, temporally high-pass filtered (0.01 Hz cutoff) and field-map distortion corrected in BrainVoyager 20.6 (Brain Innovations, Inc.).

2.3. Stimuli and experiment

Participants viewed 3 s action animations depicting one of two avatars (a boy or a man) approaching a shelf, then crouching down or jumping up to reach a target box (Fig. 1). The vignettes were viewed under one of three task instructions: attend to the actor's actions, attend to the actor's goal or attend to the actor's identity. Each vignette was constructed from 10 viewing angles, ranging from 80° (left) to 280° (right), with a 20-degree increment. The duration of the cue was 1s, followed by a 0.5 s blank interval between cue and stimuli onset, with a 2.5 s response period after the movie encoding.

Trials were separated by a 3, 4.5 or 6-s ITI, pseudorandomized within each run such that the hemodynamic response associated with each trial could be estimated independently using the least sum of squares (LSS)

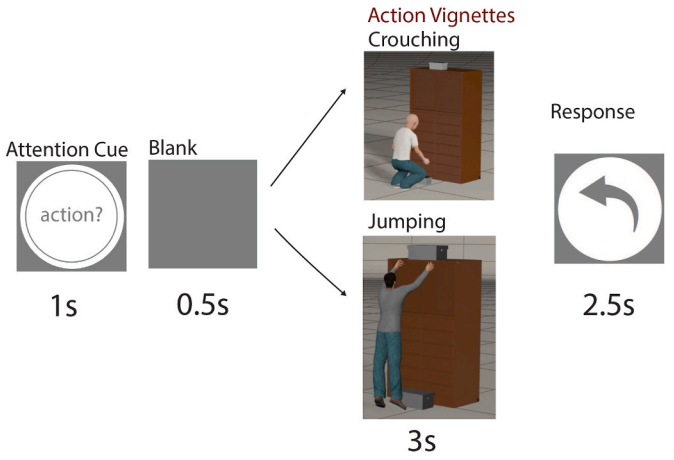

Fig. 1. Schematic of Trial Sequence. Participants were cued as to which aspect of the vignette to attend (attend to action, goal or identity). The 3 s vignette depicted an open room as an avatar approaches a shelf, directs their gaze to one of the two boxes, then either jumps or crouches to retrieve an object. Participants were prompted to discriminate the action (jump or crouch), the goal (the box positioned high or low) or the actor (man or boy) in accordance with the attention cue.

modeling approach (Mumford et al., 2012; Turner et al., 2012). Participants completed 24 trials per scan, with eight trials per attention condition per scan, and a total of eight scans.

2.4. Regions of interest

The **right pSTS** region of interest (ROI) served as the seed for functional connectivity analysis because of its importance as the perceptual hub for the AON and the ease with which it can be identified using independent localizers (Pitcher and Ungerleider, 2021; Iacoboni et al., 2001; Grossman et al., 2010). In separate scans, observers viewed 18 s blocks of point-light biological motion animations (1 s each with 0.5 s intertrial interval), alternating with 18 s blocks of motion-matched control animations. The pSTS was identified as the region on the superior temporal sulcus with a significantly stronger BOLD response (FDR, $q < 0.005$) for intact vs scrambled biological motion, identified using a group-level random-effects GLM (Fig. 2a).

IFC, PPC and STS+ were identified using a data-driven approach as the vertices on each subject's surface that were functionally connected to the seed right hemisphere pSTS during observation of the action vignettes (all attention conditions). Connectivity was computed with the beta-series method (described below) using all trials unlabeled for the attention condition, derived from functional data that was projected onto the smooth white matter surface in native subject space. The individual subject functional connectivity maps were Fisher r-z transformed then projected into a common standardized vertex space, constructed using group cortex-based alignment in BrainVoyager (Frost and Goebel, 2012). The group t-score maps were thresholded at an uncorrected $p > 0.05$ with $z > 1.96$, which was deliberately conservative to be inclusive of all possible connected vertices on the surface.

The group functional connectivity map was then subjected to dimensional reduction into regions of interest using the 360 atom Glasser atlas parcellation, which specifies labels for Brodmann's areas 44, 45, 45 b, and 47 in the IFC (Glasser et al., 2016) (Fig. 2b). The atlas was applied to native surfaces using Freesurfer's *mris_ca_label* then imported into BrainVoyager using custom library tools (https://github.com/tarrlab/Freesurfer-to-BrainVoyager), which allowed custom selection of the native functional volumes within the atlas parcels. Additionally, atlas parcels in posterior parietal (PPC), inferior frontal, or lateral and anterior temporal cortex (combined within an STS + ROI) were included if they contained vertices with significant functional connectivity to the pSTS. To avoid any potential bias derived from the alignment procedure, the overlap between functional connectivity maps and the atlas parcellation was conducted on a template pilot subject that was not included in any subsequent analysis.

2.5. Functional connectivity analysis

Functional connectivity was conducted using the beta-series method (Rissman et al., 2004) which derives trial-based estimates of BOLD activity across the duration of the scan and is particularly robust when applied in event-related designs with short ITI and stimulus duration, as in the current study (Cisler et al., 2014). Trial estimates of neural

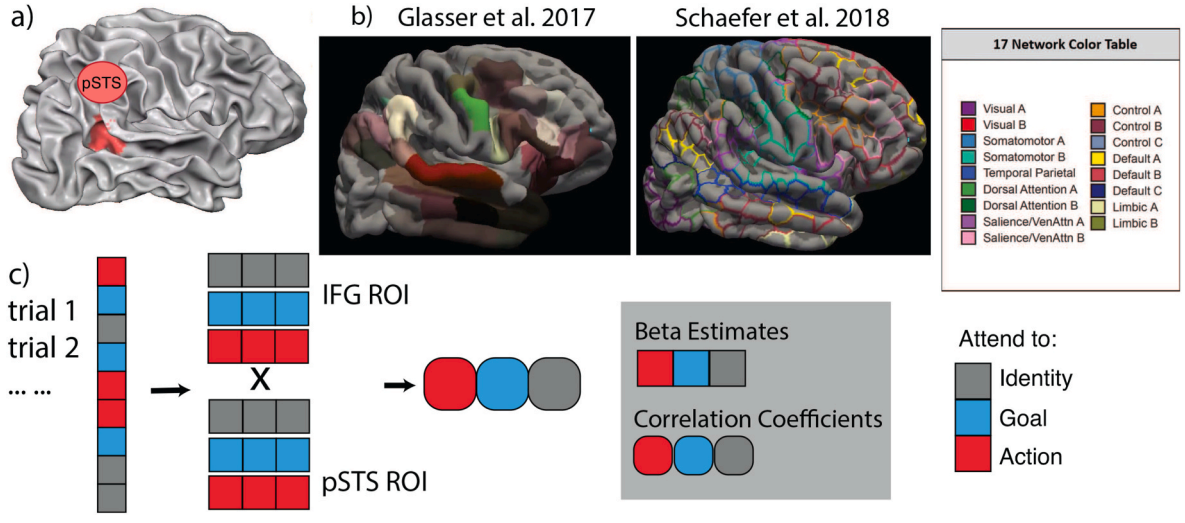

Fig. 2. Defining ROI and Connectivity Method. a) The pSTS is identified using an independent localizer and a mixed effects model that treated individual subjects as random effects. The GLM analysis was conducted on vertices in a cortex-based aligned surface space. b) Functional connectivity to the seed identified large regions of interest, each of which was further divided into smaller parcels as defined by Glasser et al. (2016). Functional systems labels for each parcel were defined using the modal network system as defined by Schaefer et al. (2018). The 17 networks in that classification were combined into eight for simpler interpretation (i.e. the dorsal attention A and B were combined into a single dorsal attention). c) Functional connectivity between two parcels was calculated using the beta-series approach in which the connectivity was computed as the correlation (circles) between the timeseries of trialwise beta estimates (rectangles). Regions of interest used this approach with trials unlabeled by task condition. The main connectivity analysis further split the trials into unique types based on the task labels.

activity were calculated using least sum of squares (LSS) design (Mumford et al., 2012; Turner et al., 2012) with all functional scans z-scored and concatenated. Trialwise beta estimates were computed using a fixed effects general linear model that iteratively modeled the predicted neural activity for one trial (a boxcar function for the 3 s duration of movie watching for that trial, convolved with a hemodynamic response function). The design matrix also captured the predicted brain response for all other trials using a single regressor modeling the expected BOLD response for all the other trials except for the current trial being modeled. The design matrix also included the following nuisance regressors: all six rigid body motion realignment parameters and their Volterra expansion, and global signal as measured from the white matter and ventricles. Trials that contained volumes with instantaneous motion (FD) greater than 0.4 mm were censored (Power et al., 2014).

Functional connectivity between regions of interest were correlations computed at the parcel level separately for three conditions: attending to action, attending to goal and attending to identity (the baseline condition in which attention is directed away from the action features). Correlations were computed between the beta-series of any two parcels (Fig. 2c), within each subject. The task-specific correlations were then Fisher r-z transformed and a pairwise *t*-test at the group level tested for significant differences in parcel-parcel connectivity as function of task.

2.6. Functional network assignment

Functional network assignment was achieved using the 17-network Yeo et al. (2011) atlas labels, which we consolidated to 8 networks (i.e. Default A, B, C combined into one network: Default). Note that there is no direct mapping between these labels and the Glasser et al. (2016) atlas. We therefore parcelled each native anatomy using the 1000 atom Schaefer system (Schaefer et al., 2018), which yields a high resolution parcellation with the associated functional system labels (Fig. 2b). Because there are unique boundaries and vertex assignments between the Glasser et al. (2016) and Schaefer et al. (2018) atlases, functional labels were assigned based on the majority network within each parcel computed using custom scripts in Matlab R2017 (Mathworks, Inc.). Additionally, any parcel without a majority network accounting for 60% or more of the vertices was identified as a "multi" system parcel. See Hartwigsen et al. (2018) and Numssen et al. (2021) for a similar data-driven approach.

3. Results

3.1. Functional connectivity to right pSTS seed

The right pSTS has been identified as a proposed input for the AON (Iacoboni et al., 2001), represents the transition from low-level sensory to higher-level cognitive representations (Pitcher and Ungerleider, 2021; Patel et al., 2019) and has the advantage of being easily identified using independent functional localizers (Grossman et al., 2010). We therefore localized the right pSTS using independent scans and identified additional regions of the AON using beta-series functional connectivity method with the right pSTS as a seed. This approach revealed three large bilateral regions of cortex with significant connectivity to the pSTS during all task manipulations: the inferior frontal cortex (IFC), a region on the lateral and anterior STS (STS+) and the posterior parietal cortex(PPC) (Fig. 3). Because the regions of interest are large and likely reflect many unique cognitive processes within, we subdivided each ROI into smaller anatomical parcels based on a template atlas applied to individual subjects. In summary, there were 23 IFC parcels, 14 STS + parcels and 6 PPC parcels identified in each hemisphere.

To characterize the dependency of connectivity in these regions on the attention task, we first compared connectivity strength during trials when the participant attended to the agent's action or goals, versus when participants attended to the agent's identity, which served as a baseline comparison condition in which attention was directed away from features that promote action understanding (Fig. 4). Note that the stimulus events in all three of these conditions were the same and only the top-down attention goals of the observer differed.

We found that many of the parcel connectivity strengths within the AON were modulated by the observer's task such that connectivity was strengthened when attending to actions as compared to the other tasks (Fig. 4, red bars). A binomial exact test comparing the functional connectivity to the pSTS when attending to action versus identity revealed significantly more parcels with stronger connectivity in the IFC ($p < 0.001$) and the STS+ ($p = 0.02$), but no significant modulations in functional connectivity between the pSTS and parietal cortex ($p = 0.51$). The comparison of attending to goal versus identity did not result in consistently modulated connectivity in any of the ROIs (binomial exact test, $p > 0.05$ for all) (Fig. 4, blue bars).

Similarly, in a direct comparison of attending to the action (the how) versus the goal (the why), we found the vast majority of parcels in the IFC and the lateral and anterior STS increased connectivity to the pSTS when the participant attended to the agent's actions as compared to the agent's goals (binomial exact test, IFC: $p < 0.001$; STS+: $p = 0.05$; Fig. 4, middle row). Those parcels with significant modulations in connectivity ($t > 1.71$, $p < 0.05$) were most frequently found between the right pSTS and right IFC (Bottom right quadrants of the polar plot). All but one parcel in the STS+ (right A4) that reached significance were more strongly connected when attending to actions as compared to goals.

3.2. Functional systems connected to the pSTS

The IFC and STS + are large ROIs that can be subdivided into many parcels and exhibit a wide range of functional heterogeneity (Hartwigsen et al., 2018). Therefore to gain deeper insights into these more

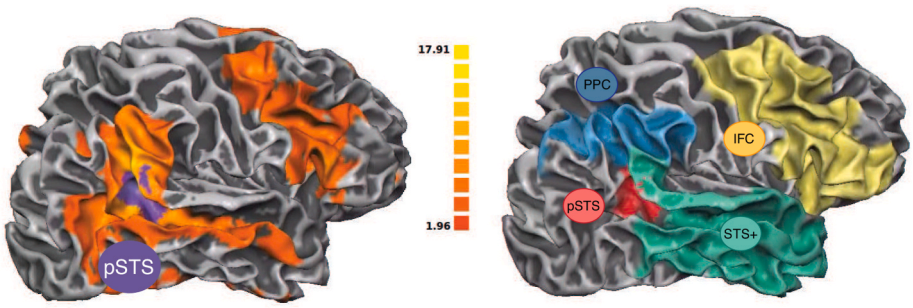

Fig. 3. ROI Identification. Left: Group-level maps of functional connectivity (z >= 1.96, p < 0.05 uncorrected) of the whole brain using the right pSTS (purple) as a seed. All trials regardless of attention manipulation were included in this analysis, which served to localize large regions of interest that were further subdivided into parcels. Right: Connectivity maps divided into regions of interest: inferior frontal cortex (IFC), posterior parietal cortex (PPC) and lateral and anterior superior temporal sulcus (STS+).

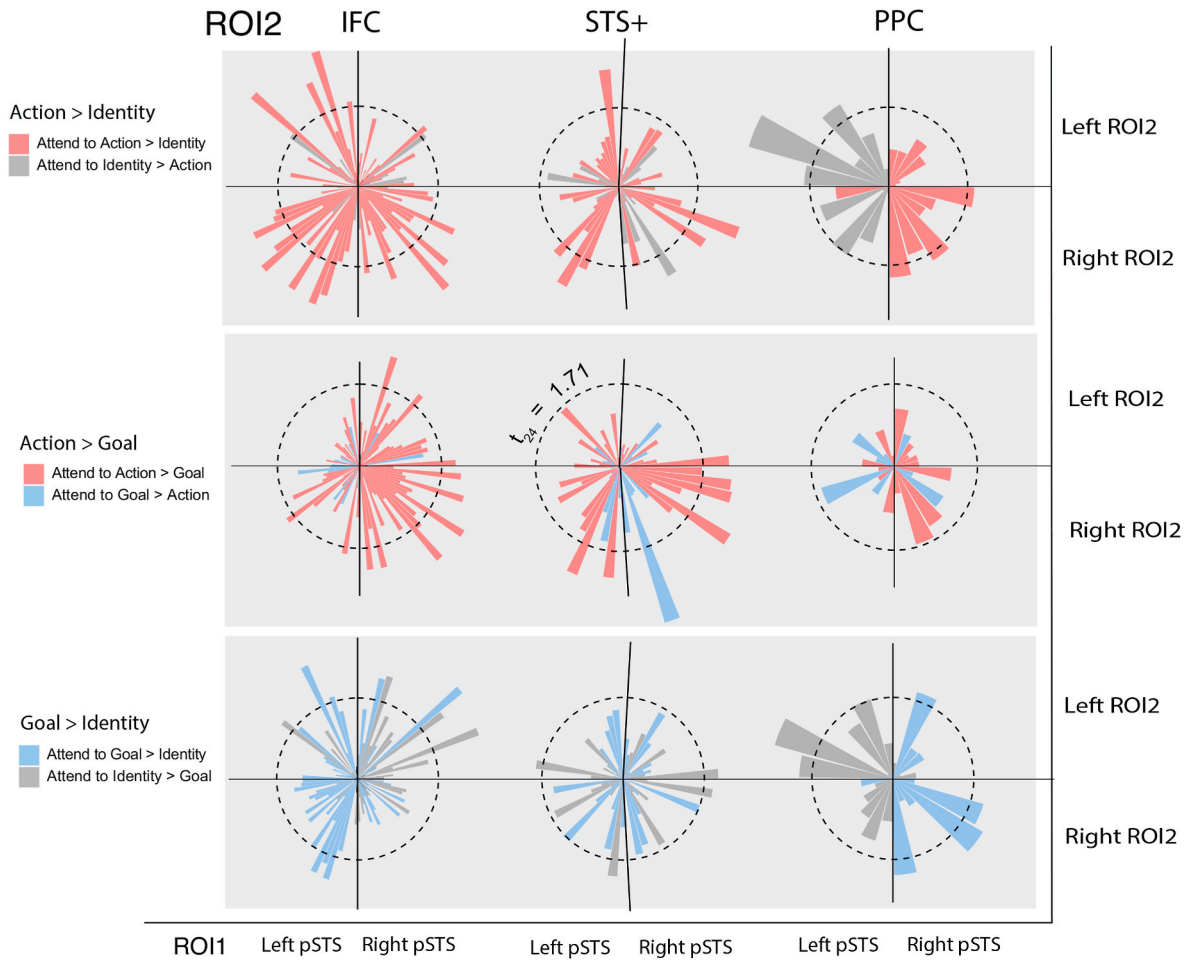

Fig. 4. Modulation of Connectivity from pSTS between pairs of tasks (attend to action, goals or identity) in the pSTS (the seed ROI) and the other ROIs. Each bar indicates the magnitude of the difference in functional connectivity strength in a single parcel, computed across participants using the pair of conditions as indicated on the left. Right and left sides of each polar plot indicate connectivity to the right and left hemisphere pSTS, respectively. Top and bottom quadrants in each polar plot specify left and right hemispheres of the target ROIs. Top row: Attending to action (red) vs identity (gray). Middle row: attending to actions (red) versus goals (blue). Bottom row: attending to goals (blue) versus identity (gray) of the actors. Dashed line indicates the statistical significance threshold ($p < 0.05$).

complex functional regions of interest, we further characterized the parcels exhibiting modulated connectivity using the functional system labels as assigned by the updated Yeo et al. (2011) functional network system (Schaefer et al., 2018).

Among those parcels with significantly modulated functional connectivity between the pSTS and IFC (shown in Fig. 5a), the dominant functional networks engaged were executive systems, including the frontal-parietal control network, the ventral attention network and the default mode network (Fig. 5b). The parcels with connectivity between the pSTS and STS + that were modulated by the task were more diverse, and included fronto-parietal control networks, the default mode network, somatomotor and limbic systems.

3.3. Functional connectivity between the IFC, PPC and STS+

In addition to examining the connectivity to the seed pSTS, we extended our investigation to explore the modulated connectivity between IFC and PPC, as well as the lateral temporal STS+. Notably, these regions are characterized by large ROIs that can be subdivided into many parcels, and exhibit a much wide range of functional heterogeneity as compared to pSTS (Hartwigsen et al., 2018; Numssen et al., 2021).

To assess the modulated functional connectivity between each parcel from the ROI pairs, we calculated and organized the connectivity results according to the functional system. Fig. 6 shows the connectivity modulations between the parcels in the IFC and the STS+ and PPC. Among those many parcels, connections that were modulated by attention (action identification greater than goal inferences) were dominated by the executive fronto-parietal control network and ventral attention system in the IFC and right PPC, with some engagement of the temporal parietal network and default mode networks in the STS+. Modulated connectivity between these regions was strongly bilateral in the IFC, but more right lateralized in the STS + when attending to actions.

3.4. The univariate BOLD response

To determine whether the increase in functional connectivity observed during action observation reflects strengthening of connections within the AON or the recruitment of additional neural populations for that task, we also evaluated the univariate response modulations for each of the parcels in our regions of interest, relative to a mean MR signal baseline (Fig. 7). We found the BOLD responses in three of the regions of interest to have BOLD amplitudes that differed when attending to goals versus actions, with all three more strongly activated by goals (right PPC: $t = 3.06$, $p < 0.01$; left PPC: $t = 1.84$, $p < 0.05$; right IFC: $t = 2.19$, $p < 0.05$). It is worth noting that although univariate response in right IFC is significantly stronger during goal inference comparing to action, this difference is mainly driven by two parcels out of 23 parcels, while the univariate response in parietal cortex is more

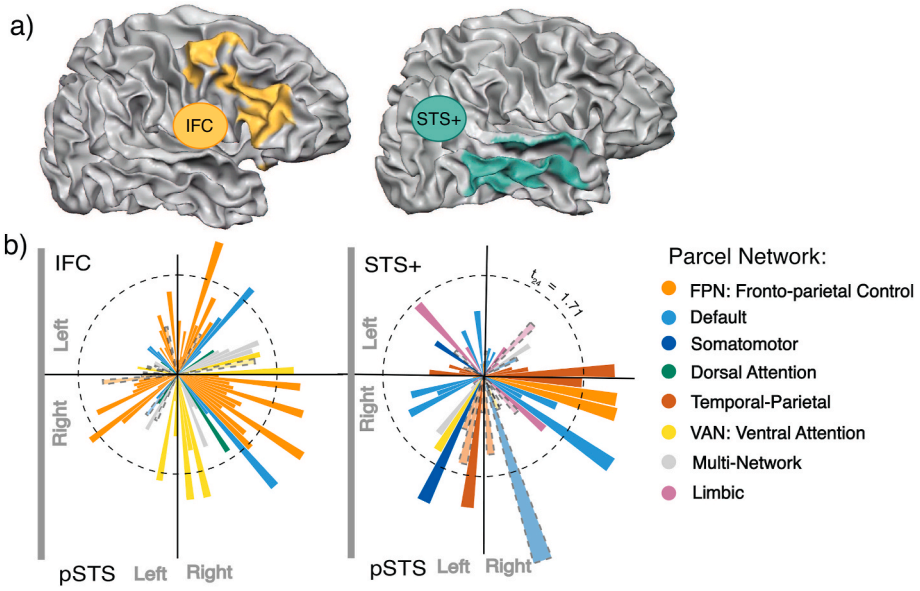

Fig. 5. Functional Network of the Modulated Connectivity. Panel a) IFC and STS + parcels with significant modulation in the strength of functional connectivity when attending to actions versus goals. Panel b) The magnitude of functional connectivity modulation (as shown in Fig. 4), colored by functional network assignment as derived from Schaefer et al. (2018). Bars with solid border have magnitude indicating stronger connectivity during actions versus goals. Bars with dashed borders indicates parcels with strong connectivity during goals as compared to actions.

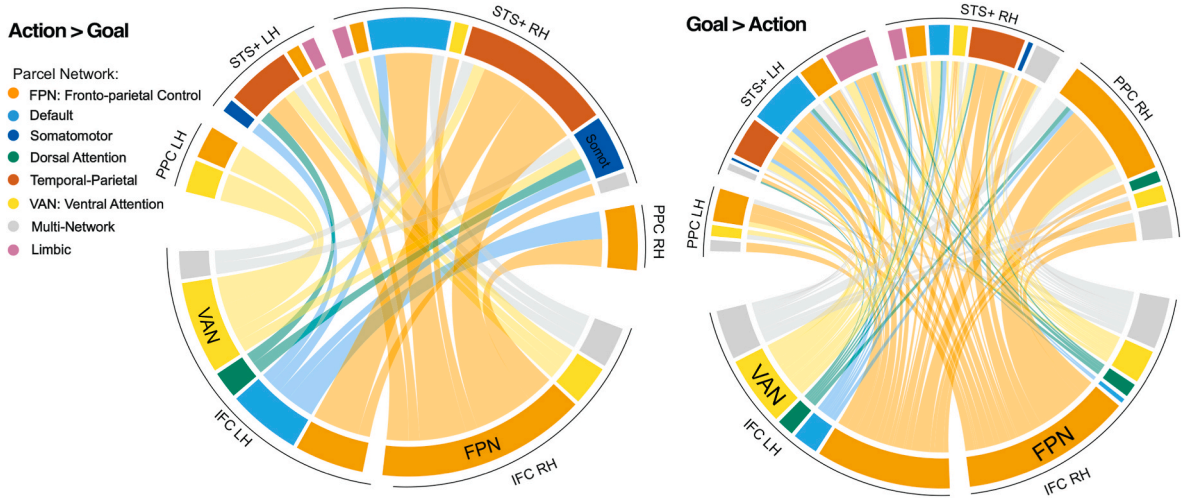

Fig. 6. Chordgram showing the functional system engaged between IFC, STS+, and PPC ROIs when subject attend to action more than goal (left) and attend to goal more than action (right). Each strand represents the proportion of connections between two functional networks that are significantly modulated ($p < 0.1$) by the attentional instruction. In each of the chordgram, colors of the strange represent the functional network as assigned from the IFC (shown on the bottom ring). Target strands are ordered as STS+ (central) to PPC (peripheral).

consistent throughout the ROI (See Supplementary Fig. 8 and Table 1). There was no effect of task on the univariate BOLD in the left IFC, bilateral pSTS or STS+.

4. Discussion

The goal of this study was to characterize how connectivity within the action observation network changes depending on the cognitive goals of the observer. We identified three large regions of interest, all functionally connected to the pSTS during action observation: the IFC, PPC and STS+. The PPC and IFC are core components of the action observation network commonly also identified as having mirror neuron properties (Caspers et al., 2010). The lateral temporal lobe, which is included as part of STS+ in our current study, is not traditionally considered part of the AON. However, the lateral STS is associated with increasing levels of abstraction in action understanding (Spunt et al., 2016) and narrative understanding in context of naturalistic viewing (Jääskeläinen et al., 2021), both of which are relevant to this study. The lateral STS+ is included in recent proposals of a conceptually-driven lateral pathway in the temporal lobe supporting semantic knowledge for action understanding, most apparent when actions are directed towards manipulating objects (Pitcher and Ungerleider, 2021; Wurm and Caramazza, 2021; Buxbaum and Kalénine, 2010b).

We found that connectivity within this extended AON was modulated by cognitive state of the observer, consistent with our previous report of sharpened representations in the pSTS when attending to kinematics (Stehr et al., 2021). In the current results we found the majority of the parcels within these large regions of interest were more strongly connected when attention was directed how the action was being accomplished (action kinematics) versus why (actor's goal). These

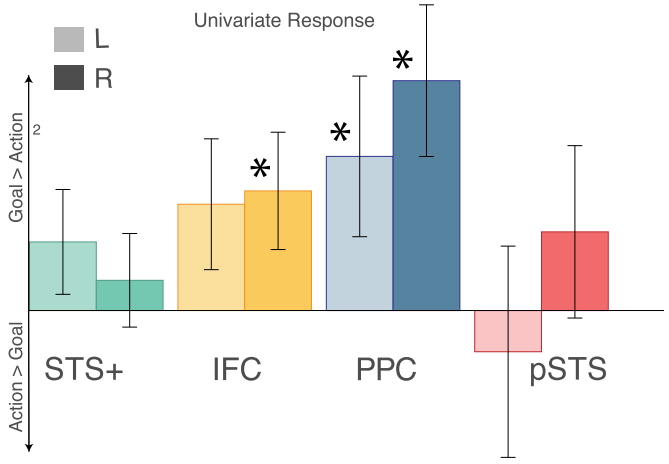

Fig. 7. Univariate Analysis Results. Univariate response modulation within each region of interest, all parcels combined. The BOLD modulation is computed as the difference in beta amplitude on trials with attention directed to goals versus action, and vice versa. Amplitude above zero indicates a stronger BOLD response for trials with attention directed to the goals versus actions in the vignettes. Scores below zero scores indicate stronger BOLD when attending to actions (versus goals). Each bar reflects the average ROI univariate response across all subjects and parcels within the ROI. Lighter colored bars show the univariate response in the left hemisphere and the darker colored bars show the BOLD response in the right hemisphere. Asterisks (*) indicated significant modulation of the BOLD response by the attention condition (in the bilateral PPC and right IFC ROIs).

modulated connections between pSTS and the IFC and STS + largely reflected the engagement of default mode network (DMN) and fronto-parietal control networks, emphasizing the importance coordinated activity of the AON with executive systems to support the observer's goals.

We do not interpret our results as evidence for more neural engagement during the different attention conditions. Stronger connectivity to the pSTS was true despite no task-related univariate modulations in the pSTS, left IFC or STS+. Only the IPL and right IFC had univariate activations modulated by task, and in both cases these regions were more strongly activated by attention directed to goals (consistent with Hamilton and Grafton, 2006, 2008). This finding highlights how coactivation and connectivity reflect two unique mechanisms of engagement, with the former reflecting robustness of the neural response and the latter reflecting coordinated network activity (Bressler and Menon, 2010). Attending to actions strengthens subpathways within the AON that target the pSTS and relevant executive control networks, and this connectivity is independent from the size of the neural population localized to each region of interest (as assessed by the univariate BOLD). Together our findings demonstrate that the cognitive state of the observer is a powerful modulator of the functional architecture of the action observation network.

In the brain, the AON is closely associated with sensorimotor neurons in premotor cortex (PMC) and the anterior intraparietal sulcus (aIPS), both implicated in observing reaching and grasping movements. The AON also includes neurons in the inferior frontal cortex that represent action concepts and goals (Grafton and Tipper, 2012; Orban et al., 2021; Molenberghs et al., 2012; Cook et al., 2014). In addition, the AON includes brain regions that support the recognition of non-grasping effectors (i.e. faces and whole bodies) and actions that are intransitive (i.e. not directed towards objects), which includes the anterior region IFC and dorsal region IPL, in addition to the posterior superior temporal sulcus (pSTS) and the posterior middle temporal gyrus (pMTG) (Caspers et al., 2010; Van Overwalle, 2009). These more posterior regions lack motor properties and instead have neural populations tuned to body and face kinematics (Pitcher and Ungerleider, 2021) and, in the left hemisphere, represent conceptual action information that generalizes broadly across stimulus formats (Wurm and Caramazza, 2021). These more perceptual and conceptual representations are proposed to serve as input to the frontoparietal systems such that they facilitate action prediction, recognition and understanding (Rizzolatti and Craighero, 2004; Iacoboni, 2005; Cook et al., 2014).

Here we find that the regions of the IFC more closely linked to action observation are parcels in the fronto-parietal, ventral attention networks and the default mode networks. Rather than motor function, we infer our results to reflect the coactivation of the AON with cognitive-executive functions of the IFC, perhapse serving as a controller for binding relevant subnetworks within AON (Spreng et al., 2010). The nature of the connectivity depends on the subject's goals and therefore the attended features during the action vignettes, which implies that the coordination of the systems promotes binding of information across established representations (Cole et al., 2013).

Our findings are consistent with the proposed dual pathway models of the action observation system (Rizzolatti and Matelli, 2003; Buxbaum and Kalénine, 2010a; Wurm and Caramazza, 2021). In these models, online visuomotor transformations are supported by a dorso-dorsal pathway that is distinct from knowledge-based representations of actions, objects and their affordances. The ventral "conceptual" pathway for action understanding is linked to semantic and conceptual knowledge representations (Binder and Desai, 2011), relating that conceptual knowledge to object affordances (Wurm and Caramazza, 2021), and to social communication more generally (Pitcher and Ungerleider, 2021). In the current study, we found the ventral conceptual pathway to be more strongly engaged by directing attention on the kinematics of the observed actions rather than attending to the actor's goals in the vignettes.

One important distinction between the proposed models of conceptual action pathways and the results obtained here is in the difference in laterality. While in our current study we found modulated pathways more strongly in the right hemisphere, in dual pathway models the ventral pathway is hypothesized to be left lateralized. For example, the left aIPS is proposed to serve as a hub for integrating visuomotor and object affordance information when observing hand-object interactions (Orban et al., 2021). Similarly, the left posterior temporal cortex is linked to action representations that generalize across verbal and visual modalities, particularly in the context of grasping actions directed

Table 1
Univariate results table showing the repeated measures *t*-test tat compares the average BOLD response between the two attention tasks. A: action, G: goal, I: identity.

Hemisphere	ROI	A > G		G > I		A > I	
		p-value	t	p-value	t	p-value	t
LH	STS+	0.13	−1.16	<0.01 *	−3.61	<0.01 *	−5.86
	IFC	0.07	−1.5	0.96	1.88	0.80	0.842
	PPC	0.04 *	−1.84	1	4.01	1.00	2.93
	pSTS	0.45	−0.12	<0.01 *	−3.66	<0.01 *	−3.81
RH	STS+	0.24	−0.709	<0.01 *	−6.34	<0.01 *	−6.6
	IFC	0.02 *	−2.19	0.38	−0.317	0.03 *	−2.02
	PPC	<0.01 *	−3.06	0.92	1.44	0.174	−0.959
	pSTS	0.21	−0.83	0.90	1.29	0.727	0.612

towards tools (Wurm and Caramazza, 2019). In contrast, the results from this study using whole-body action vignettes is more consistent with findings of right-lateralized activation in the pSTS when observing animations of bodies in action versus left-lateralized when reading action verbs (Bedny et al., 2008).

The lateral STS is not typically considered part of the canonical AON, and so we believe that there is an importance of a naturalistic context in our findings. Action animations viewed in more naturalistic settings, such as during movie watching or while listening (or reading) a narrative, are associated with bilateral activation on the lateral STS (for review, see Jääskeläinen et al., 2021). These brain regions are also among those characterized by neural populations with long temporal integration windows such that the information represented within reflects the accumulation of context extracted over long durations rather than moment-to-moment changes within a scene (Hasson et al., 2008; Chen et al., 2016; Yeshurun et al., 2017). These features are consistent with evidence that the bilateral lateral STS has neural signals that capture the essential meaning of narratives that make up episodic scenes (Baldassano et al., 2017). Related work shows that distinct regions of the bilateral lateral temporal lobe weight differentially on the unique multimodal features that carry this episodic information (Derderian et al., 2021), including actions (Lahnakoski et al., 2012). Further studies are required to more closely link the neural mechanisms of episodic narratives with the action observation network.

In conclusion, the current study reveals that goals of the observer alter network structure of the AON, both in terms of functional connectivity and univariate BOLD responses. We found that the bilateral IFC and pSTS, STS+ and bilateral pSTS had strengthened functional connectivity when subjects attended to action kinematics, while the magnitude of neural activity in the bilateral parietal cortex and right IFC was larger when attending to goals. These findings reveal two different neural mechanisms in the AON during action observation, co-activated networks versus localized changes in neural activation within regions of interest. Further, the modulated connectivity we observed was strongly right lateralized and largely involved fronto-parietal control network, indicating the importance of cognitive-executive functions in the AON. These results also suggest that the cognitive goals of the observer may strengthen cross-network connectivity between the AON with neural mechanisms that encode naturalistic action viewing in the temporal cortex.

In considering the findings of this study, it is important to acknowledge several limitations that may have influenced the results. First, our research is restricted to the use of only two types of actions, both of which involved whole bodies and were directed towards an object target. This narrow selection of actions potentially impacts the observed connectivity patterns and may limit the generalizability of our findings to a broader range of actions. It is worth noting that not all observed actions possess a specific target or object. For instance, actions like walking do not have a designated target, while social actions such as waving or hugging are directed towards living beings. This distinction between mentalizing and action should be taken into account when interpreting the results, as it may have influenced the connectivity patterns observed in our study (i.e. Van Overwalle, 2009). Another caveat to consider is the limited range of actors used, particularly the gender representation. The predominance of one gender in avatars portrayed may introduce biases or confounding factors that could influence the observed connectivity effects. Lastly, the use of avatars in our study, may have implications for the generalizability of our findings to real-world contexts. Future research should aim to address these limitations by incorporating a more diverse range of actions, considering a balanced gender representation, and employing stimuli that are more naturalistic in reflecting real-world social interactions.

CRediT authorship contribution statement

Xiaojue Zhou: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Daniel A. Stehr:** Methodology, Software, Investigation, Data curation. **John Pyles:** Resources, Funding acquisition. **Emily D. Grossman:** Conceptualization, Resources, Funding acquisition, Project administration, Supervision, Writing – review & editing.

Data availability

Data will be made available on request.

A. My appendix

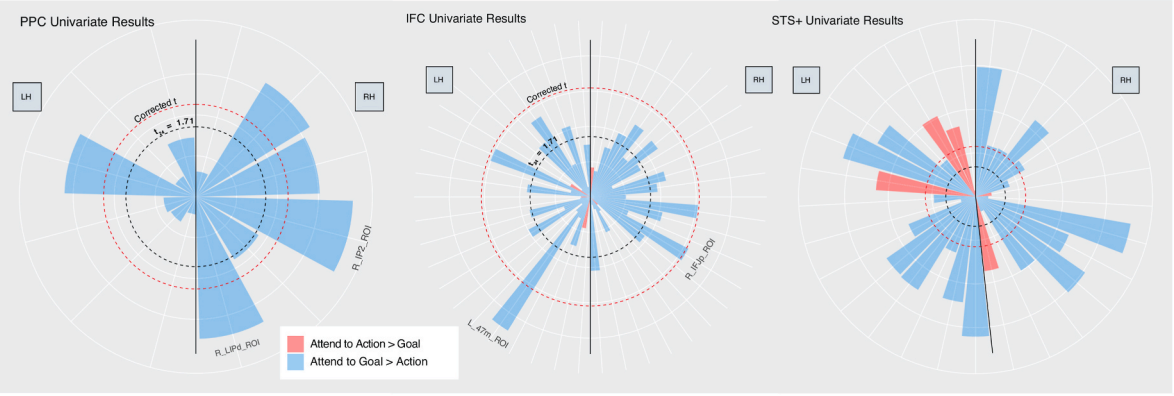

Fig. 8. Univariate response results in PPC, IFC and STS + ROI. each bar represent one parcel and the color indicates whether the response is stronger for action(red) or goal(blue).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2023.108704.

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