



A shared neural code for perceiving and remembering social interactions in the human superior temporal sulcus

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ABSTRACT

Recognizing and remembering social information is a crucial cognitive skill. Neural patterns in the superior temporal sulcus (STS) support our ability to perceive others' social interactions. However, despite the prominence of social interactions in memory, the neural basis of remembering social interactions is still unknown. To fill this gap, we investigated the brain mechanisms underlying memory of others' social interactions during free spoken recall of a naturalistic movie. By applying machine learning-based fMRI encoding analyses to densely labeled movie and recall data we found that a subset of the STS activity evoked by viewing social interactions predicted neural responses in not only held-out movie data, but also during memory recall. These results provide the first evidence that activity in the STS is reinstated in response to specific social content and that its reactivation underlies our ability to remember others' interactions. These findings further suggest that the STS contains representations of social interactions that are not only perceptually driven, but also more abstract or conceptual in nature.

1. Introduction

Social content is a driving factor of human memory and has a profound effect on social behavior. Social cognitive brain regions, including the medial prefrontal cortex (mPFC), temporoparietal junction (TPJ), and superior temporal sulcus (STS), are fundamental to social memory. These regions are activated during social memory tasks (Mitchell et al., 2004; Meyer and Collier, 2020) and their functional connectivity during rest predicts the quality of social memory consolidation (Meyer et al., 2019; Collier and Meyer, 2020). Moreover, brain regions associated with social cognition overlap with areas that have long been implicated in general episodic memory and event retrieval (Spreng and Grady, 2010). Robust neural signals across and within subjects in the mPFC, TPJ, and STS during event encoding are linked to better event memory (Hasson et al., 2008; Simony et al., 2016; Baldassano et al., 2017; Masís-Obando et al., 2022). In the same regions, activity patterns present during event encoding are reinstated during narrative free recall (Chen et al., 2017; Zadbood et al., 2017; Finn et al., 2018; Masís-Obando et al., 2022). However, it remains unknown what aspects of event memory drive the reinstatement in these regions.

While there has been much work showing shared neural patterns across perception and memory of specific types of visual content (O'Craven and Kanwisher, 2000; Wheeler et al., 2000; Reddy et al., 2010; Pearson, 2019; Steel et al., 2021), little work has been done to understand the neural basis of specific social content in memory, particularly in naturalistic settings. Social interactions are a critical part of event encoding (Dima et al., 2022) and are selectively processed in the human STS (Isik et al., 2017; Walbrin et al., 2018), even during natural movie viewing when controlling for other co-varying perceptual and social features (Lee Masson and Isik, 2021). However, the extent to which these brain regions are reinstated when people remember social interactions, and more generally the brain basis of social interaction memory, are still unknown.

Here we investigated the brain mechanisms underlying memory of others' social interactions, defined as any description of a social interaction between two or more people, during free spoken recall of a naturalistic movie in fMRI. Using voxelwise encoding analyses, we identified brain regions whose activity was predicted by social interactions during movie viewing, during free spoken recall, and cross-modally between movie viewing and recall. During movie viewing,

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social interactions are most predictive of responses in bilateral STS. During recall, we find regions across the temporal, parietal and frontal cortices that are predicted by social interactions. Interestingly, we find high cross movie-recall prediction in a specific sub-region of the mid-STS, and to a lesser extent in the temporal pole and mPFC. Together, these results suggest that a subset of the STS is reactivated specifically during social interaction memory, and that this region contains high-level amodal representations of others' social interactions.

2. Material and methods

2.1. fMRI data

We analyzed fMRI data from a prior study (Chen et al., 2017). The Princeton University Institutional Review Board approved the original study. 16 participants provided their written informed consent before the experiment. Participants viewed the first episode of the Sherlock BBC series and then freely recalled scenes in the scanner. Three functional runs of fMRI data were collected from each participant, with two runs of movie viewing and one run of movie recall (Fig. 1A–B). The duration of movie viewing was about 45 min in total, and the duration of the recall varied across participants.

A. Movie Viewing. Participants watched the first episode of the Sherlock BBC series while their fMRI activity was recorded. **B. Movie Recall.** In a separate scan session, participants described what they remembered about the movie during an unguided recall session. **C. Encoding model training on movie viewing data.** We trained an encoding model on the movie fMRI data. We labeled perceptual (orange) and social-affective (green) features, including the presence/absence of social interactions, at each time point in the movie. The model learned a linear mapping (beta weights) between each feature and the time-resolved data in each voxel. **D. Encoding model testing on movie recall data.** To examine the shared neural code between social interaction perception and memory, we tested the encoding model on the recall data. We labeled each time point of each participants' spoken recall based on whether a recalled event involved social interaction (green vector). To test the encoding model, we used the beta weight specific to viewing social interactions (β_{SI}) to predict brain activity evoked by social interactions during free spoken recall by multiplying it with the social interaction feature of a recalled event (green vector). The predicted brain activity was correlated with the true activity, which yielded a prediction performance score (Pearson r) assigned to each voxel.

2.2. fMRI data acquisition and preprocessing

In each functional run, whole-brain images (27 slices, voxel size = $4 \times 3 \times 3 \text{ mm}^3$) were collected on a 3 T Siemens Skyra scanner with a 20-channel head coil. An echo-planar T2* weighted sequence was used with the acquisition parameters of repetition time (TR) = 1500 ms, echo time = 28 ms, flip angle = 64° , and field of view = $192 \times 192 \text{ mm}^2$.

Preprocessing included correction of slice-timing and head movements, detrending of blood-oxygen-level-dependent (BOLD) signal, temporal high-pass filtering (140 s cut off), normalization to a Montreal Neurological Institute (MNI) space with voxels re-sampled to $3 \times 3 \times 3 \text{ mm}^3$, and smoothing with a 6-mm full width at half maximum Gaussian kernel. Preprocessed time series data were z-score standardized and shifted by 3 TRs from the onset to correct for the hemodynamic delay.

2.3. Movie feature annotation

To understand feature representations across the brain during movie viewing, we labeled each segment in the movie with a wide range of perceptual and social/affective features. Perceptual (visual and auditory) features included human annotations for indoor versus outdoor scenes, the presence of written words, and the presence of music, as well as algorithmically extracted features for the output of the fifth layer of the Alexnet DNN, hue, saturation, and pixel values, motion energy, the presence of a face, audio amplitude and audio pitch.

Two human raters also labeled a range of social-affective features in the movie, including the presence versus absence of a social interaction, whether or not a character was speaking, and whether or not a character on screen was engaged in mental state inference (or theory of mind). Finally, we used valence and arousal ratings from each scene, which were labeled by 119 participants on a Likert scale, in a prior study (Kim et al., 2020). The model trained on movie viewing data included all of these features to account for the variance explained by features that correlate with social interaction, such as the presence of faces and speaking (Fig. 2). This approach is better suited for assessing the contribution of the social interaction feature in predicting neural responses recorded during movie recall while taking into account correlating features. More details about the labeling procedure and distribution of features across the movie can be found in our original study (Lee Masson and Isik, 2021).

2.4. Audio transcripts and recall feature annotation

Audio recordings made during free recall were transcribed in the

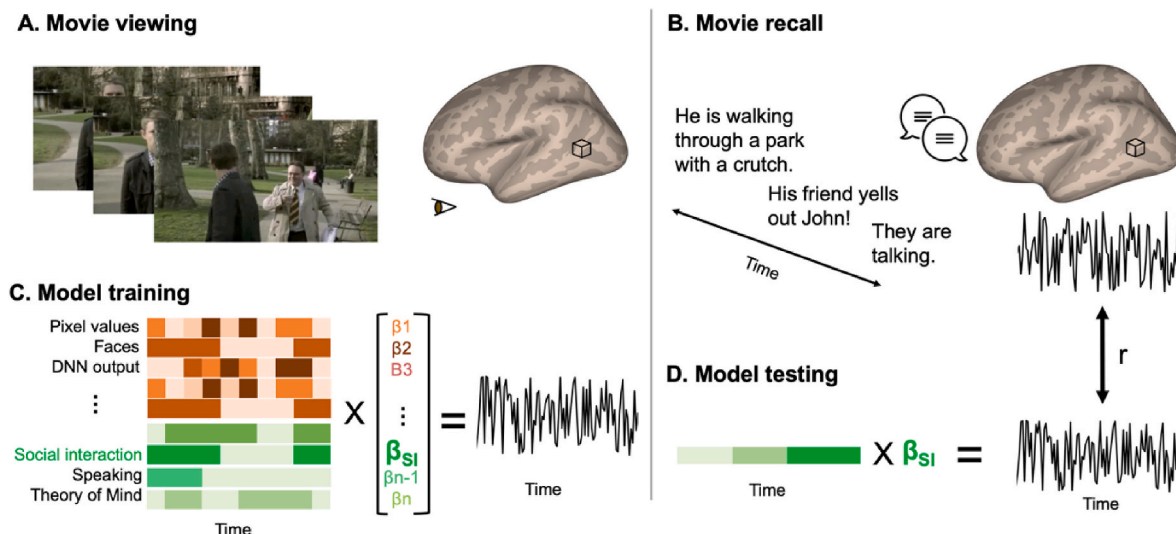


Fig. 1. Experimental procedure and cross-modal encoding framework.

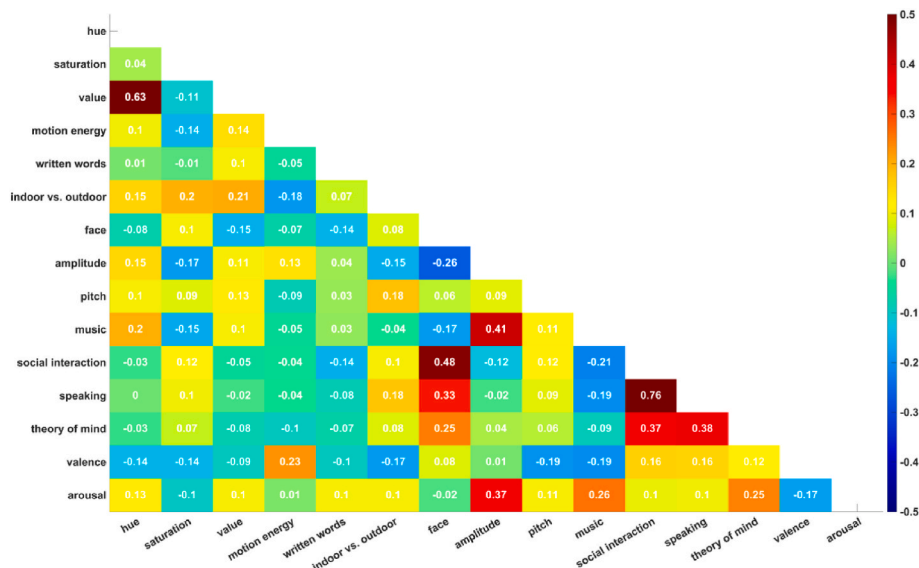


Fig. 2. Matrix showing pairwise Spearman rank correlation between movie features. Cells contains Spearman r values and are color-coded (red: positive correlation; blue: negative correlation).

original study (Chen et al., 2017). We labeled the presence versus absence of social interactions at each time point of each participant’s recall. First, we divided transcripts into sentences. Next, using a 1–5 scale, two human annotators judged whether each sentence described a social interaction (*Is a participant talking about a social interaction? 1-strongly disagree, 5-strongly agree*). Ratings were averaged and binarized (scores below 3 were labeled as non-social; scores above 3 were labeled as a social interaction). Note that judgments from the two annotators were strongly correlated ($r = 0.8$).

2.5. Movie voxel-wise encoding model

Using cross-validated encoding analyses in each individual subject (Fig. 1), we learned a linear mapping between the presence of social interactions (in addition other labeled perceptual and social movie features) and brain activity during movie viewing (model training), and then examined whether the same linear mapping could link the presence of social interactions to brain activity in held out movie data or, in the cross-modal case, recall data (model testing, see below).

Specifically, we trained an encoding model consisting of the above described perceptual and social-affective features of the movie (Fig. 1C). In each individual subject, a beta weight for each feature and voxel was estimated during training to link movie features to fMRI responses during movie viewing using 90% of the data (Lee Masson and Isik, 2021). Training data was divided into five folds. Four folds (72% of the training data) were used to estimate beta weights and optimize the regularization parameter. The remaining fold (18% of the training data) was used to select the values that produced the smallest mismatch between predicted and actual voxel-wise neural responses. After the beta estimation and regularization parameter optimization, the performance of the model was evaluated using unseen data from either the remaining 10% of movie data or entire recall data. This evaluation process was repeated ten times, and the performance was averaged across all repetitions.

We used linear banded ridge regression to account for high-dimensional features (including the output of a deep neural network) and multiple collinearities between features. Specifically, we used two different ridge penalties: one for the high-dimensional DNN features and a second for every other one-dimensional feature. To remove unreliable voxels, we excluded voxels outside of the brain mask based on inter-subject correlation (ISC) values (Fig. 3). This mask only included

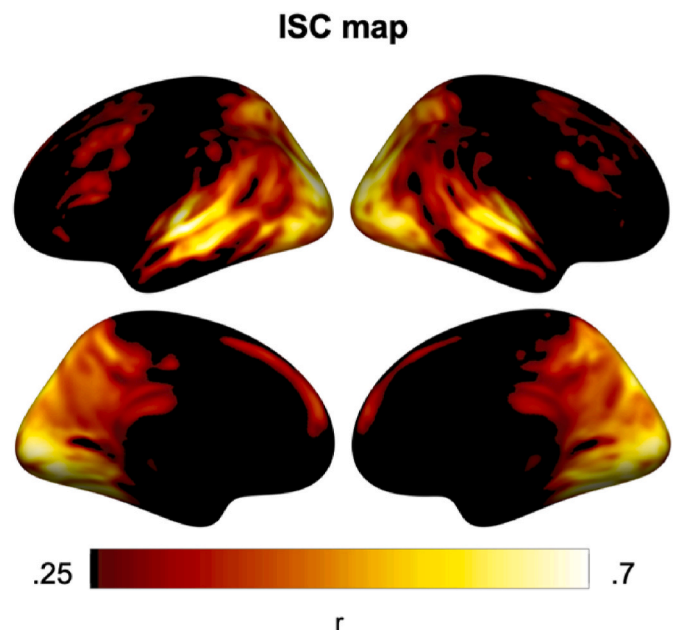


Fig. 3. Inter-subject correlation (ISC) during movie viewing. It displays the group averaged r-values. Excluded voxels ($r < 0.25$) are shown in black.

voxels showing shared stimulus-evoked responses across participants during movie viewing (ISC r value > 0.25). The threshold of r value was taken from previous work with the same Sherlock movie viewing dataset (Baldassano et al., 2017).

To examine social interaction representations during movie viewing, the learned beta weights were multiplied by the social interaction feature to predict BOLD responses in held-out movie viewing data. We calculated the prediction performance scores based on the similarity (Pearson r) between the true BOLD and estimated BOLD signals for each participant and reported average within-subject prediction.

Since the underlying distribution of the data were unknown, statistical inference was made (for this and all subsequent encoding analyses) with a sign permutation test across subjects (5000 iterations). Sign permutation can replace bootstrap permutations, and come with a lower computational cost without loss of statistical sensitivity. Both non-

parametric methods produce similar results (Lindquist et al., 2009), and sign permutations are typically used in RSA and MVPA studies to conduct nonparametric group-level statistics (Cichy et al., 2016). Note that the current method does not allow us to determine if each subject shows significantly better than chance prediction accuracy, as we base our conclusions on group-level permutation. One-tailed P values were calculated and adjusted with false discovery rate (FDR) correction. The average prediction performance was thresholded at $P_{\text{FDR}} < 0.05$ and visualized on the cortical surface using the CONN software (Whitfield-Gabrieli and Nieto-Castanon, 2012).

2.6. Recall voxel-wise encoding model

For the recall model, we trained an encoding model to link the labeled social interaction feature to voxel-wise responses in the recall data using standard ridge regression (as there was only one predictor). We trained the model on 50% of the data and tested it on the held-out 50%. All other procedures were the same as the within-movie encoding model.

2.7. Cross-modal (movie-recall) encoding model

To evaluate shared voxel representations across movie and recall, we took the encoding model trained on movie data with all labeled features, described above, and asked how well it could predict neural responses to social interactions in recall. Specifically, during testing, the beta weights learned for viewed social interactions were multiplied by the social interaction recall feature (the presence vs absence of social interactions during recall) to predict the BOLD responses recorded during movie recall (Fig. 1D).

3. Results

3.1. Neural responses to viewed social interactions in a natural movie

We extracted the learned beta weights in each voxel for the presence of a social interaction to investigate the representation of social interactions during movie viewing, while accounting for all other co-

varying labeled features. The extrastriate body area (EBA), bilateral STS, posterior medial cortex (PMC), and mPFC showed increased activation to scenes with social interactions, as observed by their positive beta weights (Fig. 4A). In contrast, scenes without social interactions activated brain areas located in visual regions across the ventral and dorsal pathways, including the inferior temporal gyrus and the inferior parietal lobe, as observed by these regions' negative social interaction beta weights. As a stronger test of social interaction representations, we asked if the learned beta weights for social interaction can predict neural responses in held-out movie data. We find significantly above chance prediction in ventral, parietal, and prefrontal cortex, with the strongest prediction bilaterally in the STS (Peak accuracy found at the MNI coordinates $X, Y, Z = -60, -27, -3$ and $51, -33, 0$) (Fig. 4B). These results confirm previous studies reporting the involvement of visual and social brain areas, particularly the EBA (Abassi and Papeo, 2020) and STS (Isik et al., 2017; Walbrin et al., 2018; Lee Masson and Isik, 2021), in social interaction perception.

3.2. Neural responses to remembered social interactions

During recall, participants spent on average 57% (range 48–68%) of their time describing remembered social interactions, further underscoring their prominence in memory. To investigate the neural basis of these social interaction memories, we trained a separate encoding model to predict fMRI data based on the presence versus absence of social interactions in each subject's recall data. The learned beta weights for social interactions in recall had some similarities to the beta weights learned on movie viewing data but were largely non-overlapping (Fig. 5A). In particular, the strong responses in person-perception areas like pSTS and EBA that were observed in the movie viewing data were not highly weighted in the recall data. Instead, the highest loadings were observed in right anterior STS and the precuneus.

Activity in these regions was also well predicted by the recall encoding model in held-out test data (Fig. 5B). Several regions that have been shown to be involved in event-specific narrative recall, including the middle occipital gyrus and parietal cortex ($X, Y, Z = -36, -84, 36$; $X, Y, Z = 42, -75, 33$), STS ($X, Y, Z = -57, -48, 15$; $X, Y, Z = 45, -36, -3$), middle frontal gyrus ($X, Y, Z = 27, 15, 54$), and posterior medial cortex

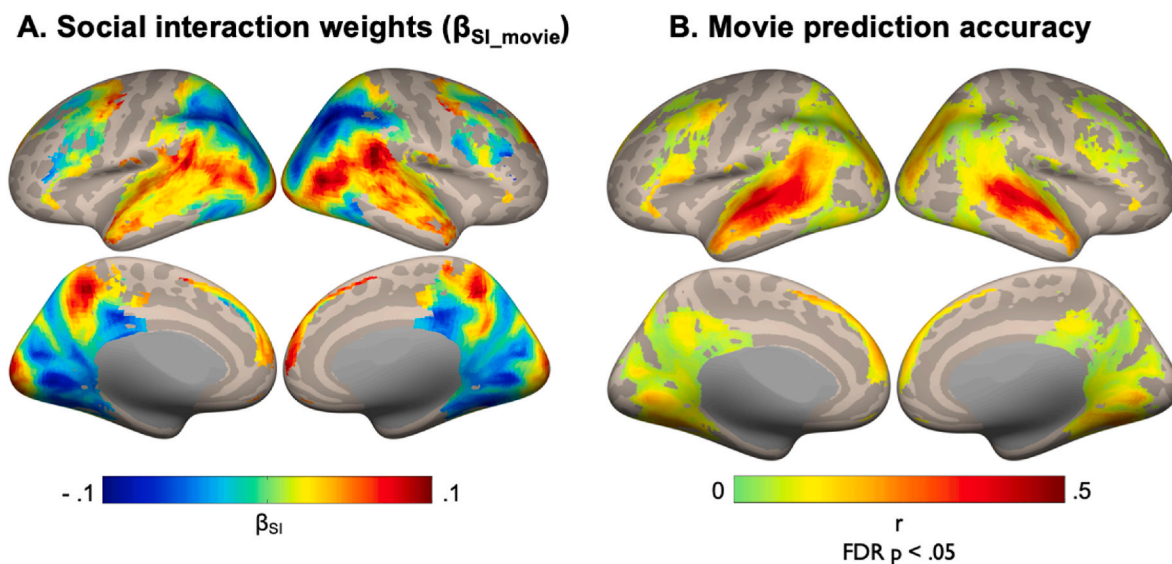


Fig. 4. Social interaction prediction (within modality) during movie viewing. A. **Social interaction weights during movie viewing.** Learned beta weights for the presence of social interactions estimated from full movie viewing encoding model mapped on an inflated cortical surface (masked to only include voxels with significant inter-subject correlation). The social interaction feature loads positively on voxels in EBA, STS, mPFC, and precuneus, shown yellow/red. Negative loadings are shown in blue/purple. B. **Social interaction prediction during movie viewing.** After false discovery rate (FDR) correction, the voxels that are significantly predicted (correlation, Pearson r) by social interactions in held-out movie viewing data are mapped on inflated cortices. Prediction accuracy was highest in bilateral STS.

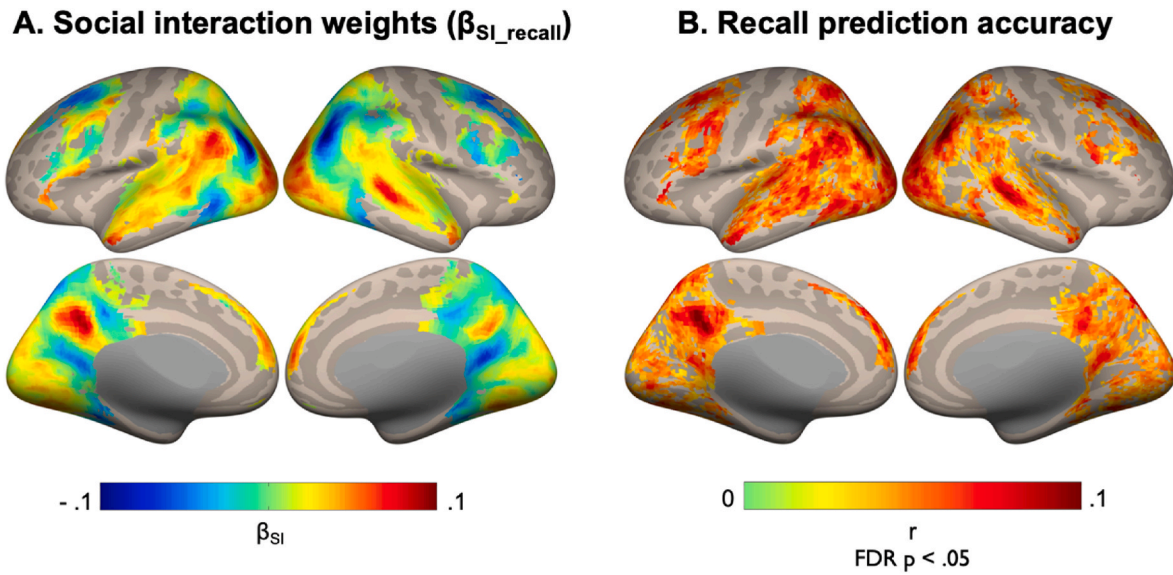


Fig. 5. Social interaction prediction (within modality) during movie recall. **A. Social interaction weights during movie recall.** Learned beta weights for the presence of social interactions estimated from an encoding model based on the presence versus absence of social interactions in recall mapped on an inflated cortical surface (masked to only include voxels with significant inter-subject correlation). The social interaction feature loads most strongly on voxels in right anterior STS and precuneus, shown yellow/red. Negative loadings are shown in blue/light blue. **B. Social interaction prediction during movie recall.** After false discovery rate (FDR) correction, the voxels that are significantly predicted (correlation, Pearson r) by social interactions in held-out recall data are mapped on inflated cortices. Prediction accuracy was highest in bilateral middle occipital gyrus, precuneus, and right STS.

(PMC) ($X, Y, Z = -9, -54, 33$), were also well predicted by our social interaction recall model. Prediction in the parietal cortex was likely due to the absence of social interactions, as indicated by the negative beta weights in that region (Fig. 5A), while all other regions are likely due to the presence of social interactions. It is important to note though that these predictions are less controlled than our movie viewing results, as recall varied from participant to participant and since no other features were labeled and fit in the recall encoding model.

3.3. Shared neural responses while viewing and remembering social interactions

We next investigated our central question: whether the linear

mapping learned to link social interactions with brain activity during movie viewing (β_{SI_movie} , Fig. 6A), could also predict brain responses to the presence of social interactions during recall (Fig. 1D). Using this cross-modal paradigm, we could accurately predict brain responses to remembered social interactions in the right temporal pole ($X, Y, Z = 51, 9, -33$), right middle occipital gyrus ($X, Y, Z = 39, -75, 33$), right angular gyrus ($X, Y, Z = 39, -72, 42$), bilateral STS ($X, Y, Z = 48, -36, -3$ and $-60, -48, 15$), and mPFC ($X, Y, Z = 6, 57, 12$ and $-6, 54, 21$) (Fig. 6B). Prediction in the middle occipital gyrus and the angular gyrus were likely due to the absence of social interactions, as indicated by the negative beta weights in those regions (Fig. 6A), while all other regions are likely due to the presence of social interactions.

The highest prediction performance was found in the right STS for

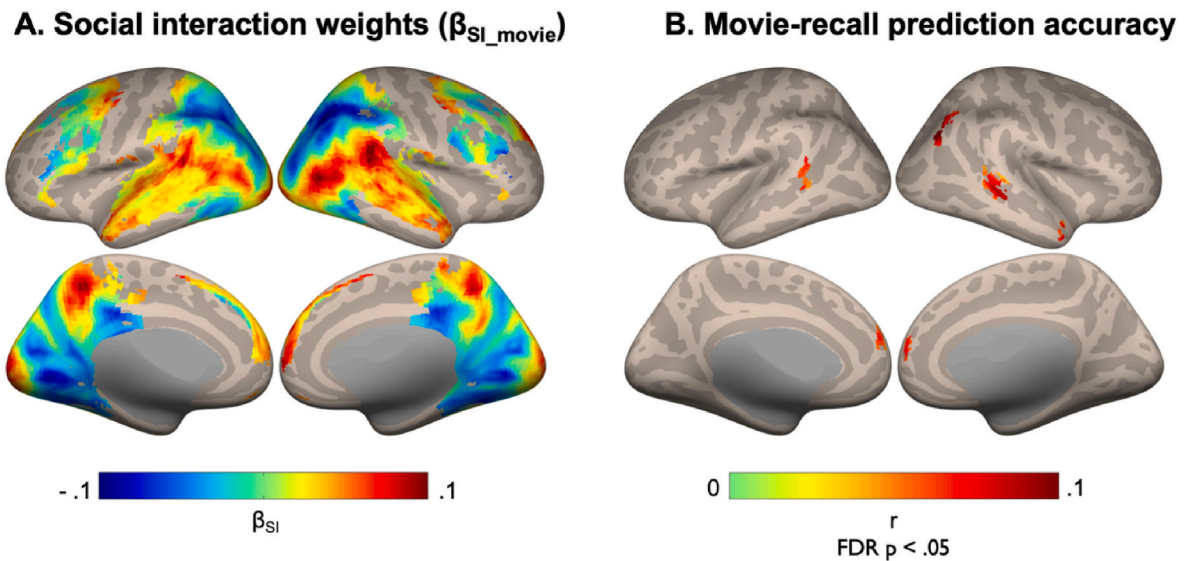


Fig. 6. Movie-trained model prediction accuracy on recall data. Panel A shows social interaction weights during movie viewing. After false discovery rate (FDR) correction, the voxels that are significantly predicted (correlation, Pearson r) by social interactions in recall using the encoding model trained on movie viewing data are mapped on inflated cortices. Prediction accuracy was highest in the right STS (panel B).

social interaction memory. Despite increased activity in the EBA during social interaction perception (Fig. 6A), we did not observe its involvement in social interaction memory. Similarly, unlike previous studies on more general narrative perception and memory (Baldassano et al., 2017; Chen et al., 2017), our results did not explain the brain activity in PMC, highlighting the specificity of our results to social interactions.

4. Discussion

In this study, we investigated the neural basis of memory for social interactions, and the extent to which these memories reactivate the brain regions engaged during social interaction perception. We first replicated prior results showing that activity along the STS is strongly predicted by social interactions in natural viewing conditions (Lee Masson and Isik, 2021). We next found that during spoken recall, social interactions were most predictive of responses in precuneus and right mid to anterior STS. Finally, by conducting encoding model analyses between movie viewing and free recall data, we found that social interaction memory leads to significant reactivation in the mid-STS, and to a lesser extent mPFC and right temporal pole.

Interestingly, the regions predicted by the cross movie-recall analysis are not simply an intersection of the regions that are best predicted by either individual model. These results add to a growing body of evidence suggesting memory retrieval is not simply a recapitulation of perception (Favila et al., 2020). For example, while large portions of the STS are significantly predicted in both unimodal encoding models, only a small subset is predicted cross-modally. Conversely, mPFC, which was only weakly predicted in the movie-viewing, data had significant cross-modal prediction. While there are other correlated stimulus factors that may contribute to prediction within movie or within recall data, these factors are absent from cross-modal encoding. Thus, this approach allows us to isolate high-level representations of social interaction that are shared across viewing and recall.

Our findings reveal that the STS is not merely involved in the perception of social interactions, but also contains amodal representations of social interactions that are engaged in the absence of any external stimulus. The posterior STS has been shown to be selectively engaged when viewing social interactions in controlled stimuli (Isik et al., 2017; Walbrin et al., 2018), and this activity was replicated in our movie viewing data (Fig. 4). Intriguingly, memory reactivation was found in a region more anterior along the mid-STS (Fig. 6), overlapping with regions showing the strongest unique selectivity to social interactions during movie viewing in our prior work (Lee Masson and Isik, 2021). This is similar to the “anterior shift” observed for memory of visual scene information (Bainbridge et al., 2021; Steel et al., 2021; Deen and Freiwald, 2022).

Cortical reactivation for sensory memories is well established, particularly for perceiving and remembering images and sounds (O’Craven and Kanwisher, 2000; Wheeler et al., 2000; Reddy et al., 2010; Breedlove et al., 2020), raising questions about the involvement of mental imagery in social interaction memory. In the current study, however, we did not find evidence of visual or auditory imagery associated with low-level perceptual features. First, participants rarely focused on the low-level perceptual aspects of social interactions during free recall (Chen et al., 2017). For example, a typical sentence describing a social interaction event during free recall might be “An old friend stops him there and reintroduces himself”. This recall lacks visual and auditory details, such as the orientation of the individuals’ bodies (e.g., facing versus non-facing) and their proximity, which play a significant role in perceiving social interaction (Papeo et al., 2019). Second, no reactivation was found in the visual or auditory cortex, not even in EBA, which was activated during social interaction encoding (Fig. 6A) and has been previously implicated in two body interaction perception (Abassi and Papeo, 2020). Likewise, given that the current encoding model was trained on neural responses from the entire movie and then tested on those from the entire free-recall session, STS may encode the general

aspects of social interaction rather than treating each social interaction scene as a distinct event. Earlier work has demonstrated that patterns of neural activity in the temporal-parietal lobe, including the STS, are reinstated in an event-specific manner during narrative-free recall (Chen et al., 2017). However, further research is required to explore the extent to which the STS shows specificity to the exact match between perceiving and remembering social interaction. Similarly, future work may investigate whether the prediction remains accurate if the model is trained on neural responses to social interactions during recall and then applied to responses from movie viewing. In the current dataset, recall time is much shorter than movie viewing time. Training a model with limited data is unlikely to yield reliable model performance. Adopting a structured or guided recall task with a longer scanning duration would better address this question. One may also question whether speech production or perception associated with self-speech during recall might have activated the STS. Given that speech production and perception do not vary systematically between recall with versus without a social interaction, it is unlikely that speech explains the STS prediction found here.

The question of whether the brain relies on a neural system responsible for general memory (semantic memory) to support social knowledge (memory for people and social behaviors) has been growing in social neuroscience (Binder and Desai, 2011). Our findings on the re-activation of the STS and its absence in the PMC suggest that social interaction retrieval may rely on specific networks of social brain regions. Prior work in episodic memory has either used simple stimuli to study specific social content (e.g., emotional faces and personally familiar versus unfamiliar faces), revealing the role of the anterior temporal pole in person-related social memory (Olson et al., 2013). Our work builds on prior findings suggesting that the neural mechanisms underlying memory retrieval may be content-specific. Further research is needed to elucidate how different types of social and non-social content are represented during memory retrieval.

Naturalistic approaches have been used to link between event encoding and memory more generally. Both approaches have highlighted the importance of cortical social brain regions, including STS, the temporal pole, and mPFC identified here. But it has been challenging to link naturalistic approaches with specific social content due to the complexity of the stimuli used in naturalistic neuroimaging (Redcay and Moraczewski, 2020; Meyer, 2023). While encoding model approaches are being increasingly used to link features to neural activity during movie viewing (Chang et al., 2021; Lee Masson and Isik, 2021; Thornton and Tamir, 2021), this is the first time such an approach has been used to isolate the neural representations for the reinstatement of specific features in memory. This approach can be generalized to content-based analyses of other aspects of social and episodic memory.

The specificity provided by our approach yields novel insight into the brain basis of social memory and contextualizes prior findings with natural stimuli. The brain areas re-activated by remembering social interactions are only a subset of those previously identified in high-level event retrieval (Baldassano et al., 2017; Chen et al., 2017). Notably absent is the PMC, which has been frequently reported in memory reactivation studies (Baldassano et al., 2017; Chen et al., 2017). The PMC may engage in more general event memory or features orthogonal to social interaction. This is in line with prior work suggesting two distinct systems for memory retrieval: the anterior temporal network for processing person-related information, and the posterior medial network for processing place-related information during recall (Reagh and Ranganath, 2023). The current work identifies one key feature of person-related memory, social interactions, that is processed in the anterior temporal network and STS. Future work is needed to understand how the neural representation of social interaction content in the STS is integrated with other types of person-related memory and more general event representations.

CRediT authorship contribution statement

Haemy Lee Masson: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **Janice Chen:** Conceptualization, Data curation, Writing – review & editing. **Leyla Isik:** Conceptualization, Funding acquisition, Supervision, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare no competing interest.

Data availability

I have shared the link to the data and the code.

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