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Social network proximity predicts similar trajectories of psychological states: Evidence from multi-voxel spatiotemporal dynamics

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ABSTRACT

Homophily is a prevalent characteristic of human social networks: individuals tend to associate and bond with others who are similar to themselves with respect to physical traits and demographic attributes, such as age, gender, and ethnicity. Recent research using functional magnetic resonance imaging has demonstrated a positive relationship between individuals' real-world social network proximity (i.e., whether they are friends, friends-of-friends, or farther removed in social ties) and inter-subject correlation (ISC) in their time series of neural responses when viewing audiovisual movies. However, conventional ISC methods only capture information about similarity in the temporal evolution of region-averaged neural responses, and ignore information carried in fine-grained, spatially distributed response topographies. Here, we demonstrate that temporal trajectories of multi-voxel response patterns to naturalistic stimuli are exceptionally similar among friends and predictive of social network proximity, over and above the effects of response magnitude fluctuations. Furthermore, inter-subject similarity in the temporal trajectory of multi-voxel response patterns across distant points in time was particularly positively associated with individuals' proximity in their real-world social network. The fact that exceptional similarities among friends were most pronounced in long-range temporal fluctuations of response patterns located in multimodal cortical regions (e.g., regions of posterior parietal cortex) suggests that aspects of high-level processing during naturalistic stimulation may be particularly similar among friends. Given the localization of results, we speculate that socially close individuals may be particularly similar in endogenously driven shifts in how they distribute their attention (e.g., across the environment, within internal representations) over time. These results suggest that friends may experience exceptionally similar trajectories of psychological states when exposed to a common stimulus, and, more generally, that there are meaningful individual differences in the temporal evolution of multi-voxel response patterns during naturalistic stimulation.

1. Introduction

Homophily (i.e., the tendency to surround oneself with similar others) is a pervasive characteristic of human social networks: friendships tend to be formed between people who are similar to one another with respect to such variables as age, gender, ethnicity, religion, and other demographic attributes (McPherson et al., 2001). Homophily has been documented across a diversity of human social groups, including across disparate geographic locations and in online communities, and has been suggested to have characterized human social networks since well before the advent of modern industrialized societies (Apicella et al., 2012; Fu et al., 2012; Lewis et al., 2012; McPherson et al., 2001). In addition to the consistent evidence demonstrating that friends tend to be exceptionally similar in terms of physical traits and demographic attributes, homophily with respect to some sociobehavioral tendencies has also been observed. For example, friends have been shown to have especially similar behavioral tendencies related to altruism and cooperation (Apicella et al., 2012; Gilchrist, 2007).

The prevalence of homophily with respect to certain demographic attributes and behavioral tendencies may be due to the fact that such similarities reflect commonalities in how people perceive, think about, and react to the world around them. Indeed, people are attracted to others who share similar values and interests to their own (Clore and Byrne, 1974). Associating with people who interpret and respond to the

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world similarly to oneself has also been suggested to be adaptive, since it facilitates effective communication (Berger and Calabrese, 1975), empathy (Krebs, 1975), and cooperation (Chiang and Takahashi, 2011; Riolo et al., 2001), and thus could promote collective action and cohesion in human groups. Such an explanation rests on the assumption that homophily in human social networks extends to internal similarities in how people attend to, make sense of, and react to the world around them.

Assessing similarities in self-reported personality traits is one way to test for such "deeper" similarities among friends, and more generally, among people who are closer together in social networks. For example, two of the "Big Five" personality traits, extraversion and openness to experience, have been shown to be more similar among friends than among those who are not friends (Feiler and Kleinbaum, 2015; Selfhout et al., 2010). However, tests for homophily based on other self-reported personality traits (e.g., agreeableness, neuroticism, conscientiousness) have yielded negative or inconsistent results (Feiler and Kleinbaum, 2015; Selfhout et al., 2010; Selfhout et al., 2009). This is at odds with the compelling intuition that many people have about friendship: individuals commonly believe that they share similarities with their friends that transcend surface-level characteristics, such as demographic variables.

It is possible that commonalities exist in how people who are relatively close together in their social networks (e.g., friends) perceive and interpret the world that are not fully captured by self-report surveys. For example, recent evidence suggests that friends have exceptionally similar linguistic styles (Kovacs & Kleinbaum, In press). Functional neuroimaging data (e.g., functional magnetic resonance imaging, fMRI) acquired while people are shown naturalistic stimuli (e.g., audiovisual movies) can provide an additional information-rich window into people's mental processing of the world around them. When it comes to effectively capturing individual differences in mental processing, functional neuroimaging during naturalistic stimulation offers several benefits over self-report measures, such as capturing mental processes contemporaneously as they unfold (rather than participants' later reflections on such processes), circumventing the need to ask participants to introspect about their own mental processes (which is often inaccurate; Wilson and Nisbett, 1978; Wilson, 2002), and avoiding self-presentation concerns (which can distort experimental results in a variety of ways; King and Bruner, 2000). In addition, whereas self-report measures are generally constrained to a limited number of targeted questions, whole-brain functional neuroimaging data acquired during free-viewing of naturalistic stimuli simultaneously measures brain activity associated with whatever perceptual, cognitive, and affective processes stimuli elicit in viewers, as those processes unfold over time. Thus, fMRI studies using unconstrained viewing of naturalistic stimuli provide researchers with the opportunity to assess many aspects of everyday mental processing in parallel in a relatively unobtrusive manner.

A considerable body of research has shown that interpersonal similarities in fMRI responses to naturalistic stimuli capture meaningful interpersonal similarities in how people attend to and understand what they see and hear. Many such studies have involved experimental manipulations of participants' goals or beliefs before they are exposed to stimuli. For example, Lahnakoski et al. (2014) instructed different groups of participants to adopt different psychological perspectives (e.g., of a detective attempting to determine who had committed a crime, or of a decorator interested in aesthetic qualities of sets) while watching the same television show. Inter-subject correlation (ISC) of fMRI response time series was higher among participants who had been instructed to adopt the same psychological perspective in brain regions associated with high-level visual processing (e.g., lateral occipital cortex; ventral temporal cortex) and top-down attentional allocation (e.g., superior posterior parietal cortex), likely reflecting differences in how participants who were asked to adopt different psychological perspectives attended to, interpreted, and stored perceptual information while watching the video. Similarly, Yeshurun et al. (2017) manipulated participants' beliefs before they listened to an ambiguous story during fMRI scanning and found that fMRI response time series were more similar in a variety of brain regions (e.g., in the default mode network and mirror neuron system) among participants who had been led to interpret the story similarly. Thus, prior work has demonstrated that when different groups of people are directed to attend to or interpret the same stimulus in diverging ways, corresponding differences in mental processing can be measured with ISC of fMRI response time series.

Additional research has shown that ISC of fMRI responses to naturalistic stimuli is also sensitive to intrinsic individual differences in how people spontaneously process the world around them (as opposed to experimentally manipulated differences). For example, subjects with autism spectrum disorder exhibit idiosyncratic fMRI responses to naturalistic stimuli relative to neurotypical subjects (Byrge et al., 2015; Hasson et al., 2009), and a burgeoning line of recent research has demonstrated the utility of ISC in capturing individual differences in neurotypical subjects' mental processing of naturalistic stimuli (Finn et al., 2018; Nguyen et al., 2019).

Thus, neural response time series evoked when people are shown naturalistic stimuli provide a rich window into people's unconstrained processing of those stimuli. Such processing varies as a function of people's dispositional traits, goals, and values, as well as their pre-existing knowledge and assumptions. If friendship, and more generally, social network proximity (i.e., whether people are friends, friends-of-friends, or farther removed in social ties), is associated with similarity in how people attend to, interpret, and respond to their environment, then social network proximity should be associated with similarity of real-time mental responding. Consistent with this possibility, it was recently found that social network proximity is positively associated with similarity in the temporal evolution of region-averaged neural response magnitudes evoked by naturalistic stimuli, particularly in brain regions related to processes such as attentional allocation, narrative interpretation, and affective responding (Parkinson et al., 2018).

As summarized above, inter-individual similarity in time series of neural responses to naturalistic stimuli captures meaningful similarity in how people attend to and make sense of their environment and is related to the positions people occupy in their real-world social networks. Importantly, the vast majority of research investigating time series of neural responses to naturalistic stimuli has looked only at how univariate response magnitude rises and falls over time, either within individual voxels (e.g., Byrge et al., 2015; Lahnakoski et al., 2014; Nguyen et al., 2019; Yeshurun et al., 2017) or averaged across voxels within brain regions (e.g., Parkinson et al., 2018; Cantlon and Li, 2013; Yeshurun et al., 2017). Yet, an abundance of literature applying multi-voxel pattern analysis (MVPA) to fMRI data has highlighted the importance of looking not only at univariate response magnitude, but also at spatially distributed response topographies (Haxby et al., 2014; Norman et al., 2006). Recent research has suggested ways to integrate ISC and MVPA approaches, for example, by comparing individuals in terms of how multi-voxel response patterns in corresponding brain regions fluctuate over time (e.g., Chang et al., 2018; Nastase et al., 2019; Rapuano et al., 2019). To the extent that the distributed response pattern within a brain region at a given point in time can be considered an approximate index of the psychological state subserved by that brain region at that time point, such analyses can provide a window into how individuals' psychological states evolve over time, with more similar response patterns indicating more similar psychological states.

In the current study, we capitalized on endogenous individual differences in neural responses to naturalistic stimuli and tested if and where inter-subject similarity in psychological states, as indexed by temporal trajectories of multi-voxel response patterns, increases as a function of proximity in a real-world social network. The current results suggest that there are meaningful endogenous individual differences in the temporal evolution of multi-voxel response patterns to naturalistic stimuli. Furthermore, they demonstrate that social network proximity is significantly associated with similarity in the temporal trajectory of spatially distributed response topographies in areas of the dorsal attention network (specifically, in the superior parietal lobule, SPL). Thus, friends, and more generally, people who are closer together in their real-world social networks, may be exceptionally similar in how their attentional states evolve over time when perceiving and interpreting the world around them.

2. Materials and methods

The data reported here were also used in a previously published study (Parkinson et al., 2018), and were reanalyzed in the current study. A more detailed description of the data collection procedures is provided in the initial publication; here, we provide a concise description of the aspects of data collection that are most relevant to the new analyses. The initial publication used conventional ISC methods, which are focused on response magnitude fluctuations and ignore information contained in distributed spatial patterns of neural activity. In contrast, the current paper is specifically focused on spatially distributed response patterns (regardless of their overall magnitude), and in particular, on individual differences in how such patterns evolve over time during naturalistic stimulation.

2.1. Social network characterization

All data collection procedures were completed in accordance with the standards of the local ethical review board. First, the social network of 279 (89 females) first-year students in a graduate program at a private university in the United States was characterized (Fig. 1). All students in the cohort completed an online social network survey (i.e., a 100% response rate was obtained), which was administered 3–4 months after they had first arrived on campus. In this particular graduate program, students lived in close proximity to each other in an isolated, rural area. Furthermore, they took classes together and frequently ate meals and socialized together. Taken together, these characteristics of this graduate program engendered an intense social experience in which the formation of meaningful friendships was likely promoted to an exceptional extent, even within a relatively short period of time (i.e., during the 3–4 months between the beginning of the academic program and the social network data collection). Subjects followed an e-mailed link to the study website where they responded to a survey designed to assess their position in the social network of students in their cohort of the academic program. The survey question was adapted from Burt (1992) and has been previously used in the modified form used here (Feiler and Kleinbaum, 2015; Kleinbaum et al., 2015; Parkinson et al., 2017). It read, *"Consider the people with whom you like to spend your free time. Since you arrived at [institution name], who are the classmates you have been with most often for informal social activities, such as going out to lunch, dinner, drinks, films, visiting one another's homes, and so on?"* A roster-based name generator was used to avoid inadequate or biased recall. Subjects indicated the presence of a social tie with an individual by placing a checkmark next to his or her name. Subjects could indicate any number of social ties, and had no time limit for responding to this question.

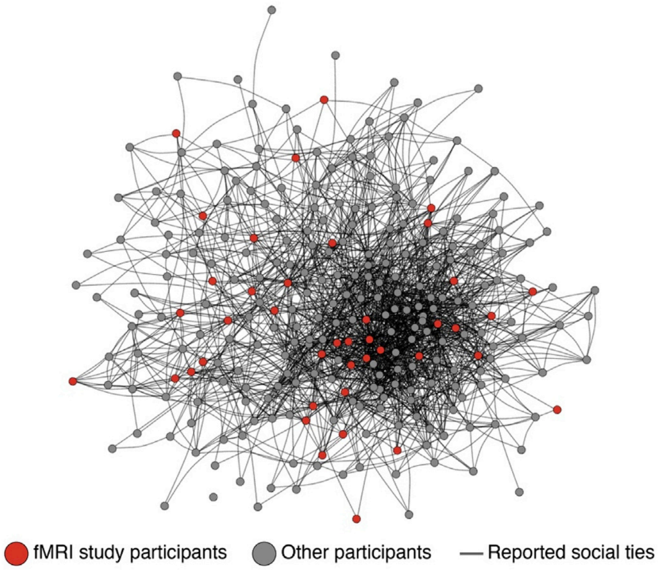

Fig. 1. Social network characterization. An entire cohort of first-year graduate students completed a survey in which they indicated their social ties with other students ($N = 279$; 100% response rate). Their social network was reconstructed using this data. Nodes indicate students, and lines reflect mutually reported ties between students. A subset of students (red nodes; $N = 42$) participated in the fMRI study.

The social network data was analyzed using igraph in R (Csárdi and Nepusz, 2014). An unweighted graph consisting of mutually reported social ties was used to estimate social distances between individuals. In other words, an undirected edge would connect two actors only if they had both nominated one another as friends. We decided to only consider mutually reported ties because we reasoned that whereas a single participant's responses on the social network questionnaire may have been impacted either by an idiosyncratic interpretation of the question (e.g., using an exceptionally strict or liberal internal criterion when responding; consistent with this possibility, out-degree centrality varied widely in this social network, ranging from 2 to 146) or errors when responding (e.g., selecting an unintended name from the list of 279 students due to inattention), mutually reported friendships were more likely to correspond to meaningful relationships. Social distance was defined as the geodesic distance between people in the social network – i.e., as the smallest number of intermediary social ties required to connect them in the network. Pairs of individuals who both named one another as friends were assigned a social distance of one. Individuals would be assigned a distance of two from one another if they had a mutually reported friendship with a shared friend, but were not friends with one another, and so on. Of the 861 dyads of fMRI participants, 63 (7.32%) were characterized by a social distance of one (i.e., they were friends), 286 (33.22%) were characterized by a social distance of two (i.e., they were friends of one another's friends), 412 (47.86%) were characterized by a social distance of three, 98 (11.38%) were characterized by a social distance of four, and two (0.23%) were characterized by a social distance of five. Given that there were only two dyads characterized by a social distance of five, dyads characterized by social distances of four and five were collapsed into a single social distance level (i.e., distance 5 dyads were assigned a value of 4) in subsequent statistical analyses.

2.2. fMRI study subjects

Forty-two subjects (12 female; 3 left-handed) aged 25–32 ($M = 27.98$; $SD = 1.72$) belonging to the academic cohort whose social network had been characterized (as summarized in Section 2.1) completed a subsequent neuroimaging study. All subjects were fluent in English and had normal or corrected-to-normal vision. Data collection for the neuroimaging study took place approximately 3 months after the collection of the social network data due to scheduling and participant availability constraints. In these three months, friendships among participants may have changed. However, we note that such changes could only have introduced noise into our estimates of distance between individuals at the time of the fMRI study and thus, reduced our sensitivity for detecting potential relationships between social network proximity and neural response similarity.

2.3. fMRI data acquisition

Subjects were scanned using a 3 T Philips Achieva Intera scanner with a 32-channel head coil. An echo-planar sequence (35 ms echo time (TE);

2000 ms repetition time (TR); 3.0 mm × 3.0 mm × 3.0 mm resolution; 80 × 80 matrix size; 240 × 240 mm field of view (FOV); 35 interleaved transverse slices with no gap; 3.0 mm slice thickness) was used to acquire functional images. Stimuli were presented over the course of six functional runs. Functional data acquisition time totaled approximately 33.7 min. A high-resolution T1-weighted anatomical scan was also acquired for each subject (8.2 s TR; 3.7 ms TE; 240 × 187 FOV; 0.938 mm × 0.938 mm × 1.0 mm resolution) at the end of the scanning session. Foam padding was placed around subjects' heads to minimize head motion.

2.4. fMRI study paradigm

Before the fMRI study began, subjects were told that they would be watching a set of videos while being scanned, which would vary in content, and that their experience in the study would be akin to watching television while someone else "channel surfed." All participants saw the same clips in the same order (as if the clips comprised different scenes of a continuous movie), to avoid inducing response variability between subjects related to differences in how clips were presented.

2.5. fMRI study stimuli

Stimuli consisted of 14 videos presented with sound over the course of six fMRI runs. Videos ranged in duration from 88 to 305 s (see Table S1 for brief descriptions of stimuli). Criteria used to select stimuli are described in more detail elsewhere (Parkinson et al., 2018). Briefly, efforts were made to select stimuli that (1) most participants would not have seen before, (2) would be engaging for participants, and (3) would evoke diverging inferences and patterns of attentional allocation across viewers, and thus, psychologically meaningful variability in neural responding (e.g., because different people might attend to, emotionally react to, and/or interpret them differently).

2.6. Preprocessing of neuroimaging data

fMRIPrep version 1.3.2 was used for anatomical and functional data preprocessing (Esteban et al., 2019). Each subject's T1-weighted (T1w) image was corrected for intensity non-uniformity with N4BiasFieldCorrection, distributed with ANTs 2.1.0, and used as T1w-reference throughout the workflow. The T1w-reference was then skull-stripped with a Nipype implementation of the antsBrainExtraction.sh workflow (from ANTs), using OASIS30ANTs as target template. Spatial normalization to the ICBM 152 Nonlinear Asymmetrical template version 2009c (MNI152NLin2009cAsym) was performed through nonlinear registration with antsRegistration (implemented in ANTs 2.1.0), using brain-extracted versions of both T1w volume and template. Brain tissue segmentation of cerebrospinal fluid (CSF), white-matter (WM), and gray-matter (GM) was performed on the brain-extracted T1w using FSL FAST.

For each of the six BOLD runs per subject, the following preprocessing was performed. First, a reference volume and its skull-stripped version were generated using a custom methodology of fMRIPrep. The BOLD reference was then co-registered to the T1w reference using FSL FLIRT with the boundary-based registration cost-function (BBR). Co-registration was configured with nine degrees of freedom to account for distortions remaining in the BOLD reference. Head-motion parameters with respect to the BOLD reference (transformation matrices, and six corresponding rotation and translation parameters) were estimated before any spatiotemporal filtering using FSL MCFLIRT. Automatic removal of motion artifacts using independent component analysis (ICA-AROMA) was performed on the preprocessed BOLD in MNI space time-series after removal of non-steady state volumes and spatial smoothing with an isotropic, Gaussian kernel of 6 mm full-width at half-maximum. The BOLD time-series were then resampled to MNI152NLin2009cAsym standard space, generating a preprocessed BOLD run in MNI152NLin2009cAsym space.

The confounding variables generated by fMRIPrep that were used as nuisance variables in the current study included global signals extracted from within the CSF, WM, and whole-brain masks, framewise displacement, three translational motion parameters, three rotational motion parameters, a basis set of cosine functions up to a cutoff of 128s, and a set of physiological noise regressors that were extracted to perform component-based noise correction (anatomical CompCor, aCompCor). More specifically, aCompCor variables were calculated within the intersection of a subcortical mask (created by heavily eroding the brain mask) and the union of the CSF and WM masks. These confounds were regressed out of the data for each preprocessed run.

2.7. Regions-of-interest parcellation

In the current study, we used the Schaefer et al. (2018) parcellation scheme (resampled to MNI152NLin2009cAsym standard space) with 200 parcels, each of which is associated with one of brain networks from the Yeo et al. (2011) seven-network parcellation– the visual, somatomotor, dorsal attention, ventral attention, limbic, frontoparietal task control, and default mode networks (Fig. 2a).

2.8. Inter-subject similarity in temporal trajectory of multi-voxel response patterns

For each subject, the preprocessed time-series data were concatenated across all six fMRI runs. In each of the 200 parcels, multi-voxel response patterns were extracted at each time point (i.e., at each TR), and the following analysis was performed independently for each of the 200 parcels (Fig. 2). We calculated the pairwise Pearson correlations between multi-voxel response patterns at each time point (Fig. 2a) in order to construct a time point-by-time point matrix ($n = 1088$ TRs) that captures the trajectory of multi-voxel patterns over time within each subject (Chang et al., 2018; Nastase et al., 2019; Rapuano et al., 2019). Each element of this temporal trajectory matrix reflects the degree to which multi-voxel patterns are correlated at each pair of TRs (Fig. 2b and c). The off-diagonal half of the temporal trajectory matrix (i.e., the upper or lower triangle, excluding the diagonal) was then submitted to subsequent analyses.

In the temporal trajectory matrix, elements closer to the main diagonal reflect pairwise correlations between multi-voxel response patterns that occur closer in time to one another, whereas elements farther from the main diagonal reflect pairwise correlations between multi-voxel response patterns that are farther removed from one another in time. Thus, in the current study, we refer to elements *closer* to the main diagonal of the temporal trajectory matrix as reflecting the *temporally proximal trajectory* of multi-voxel response patterns. Similarly, we refer to elements *farther* from the main diagonal of the temporal trajectory matrix as reflecting the *temporally distal trajectory* of multi-voxel response patterns. In order to separately analyze the temporally proximal and temporally distal trajectory of multi-voxel response patterns, we identified a diagonal parallel to the main diagonal of the full pattern trajectory structure that would split the off-diagonal half into two components approximately equal in size (Fig. 3). This diagonal split the off-diagonal half of the temporal trajectory matrix into two approximately equivalently sized components at TR 320 (out of 1088 TRs), as indicated by the dashed line in Fig. 3a. The component closer to the main diagonal of the full temporal trajectory matrix is defined as the *temporally proximal pattern trajectory structure* (Fig. 3c), whereas the component farther from the main diagonal is defined as the *temporally distal pattern trajectory structure* (Fig. 3b). Combined, these two component structures comprise the *full pattern trajectory structure* (i.e., the entire off-diagonal), which reflects the temporal trajectory of multi-voxel patterns over all time points (Fig. 3a).

We then conducted three separate analyses: we tested the relationship between social network proximity and inter-subject similarity in subjects' (1) full temporal trajectory, (2) temporally proximal trajectory, and

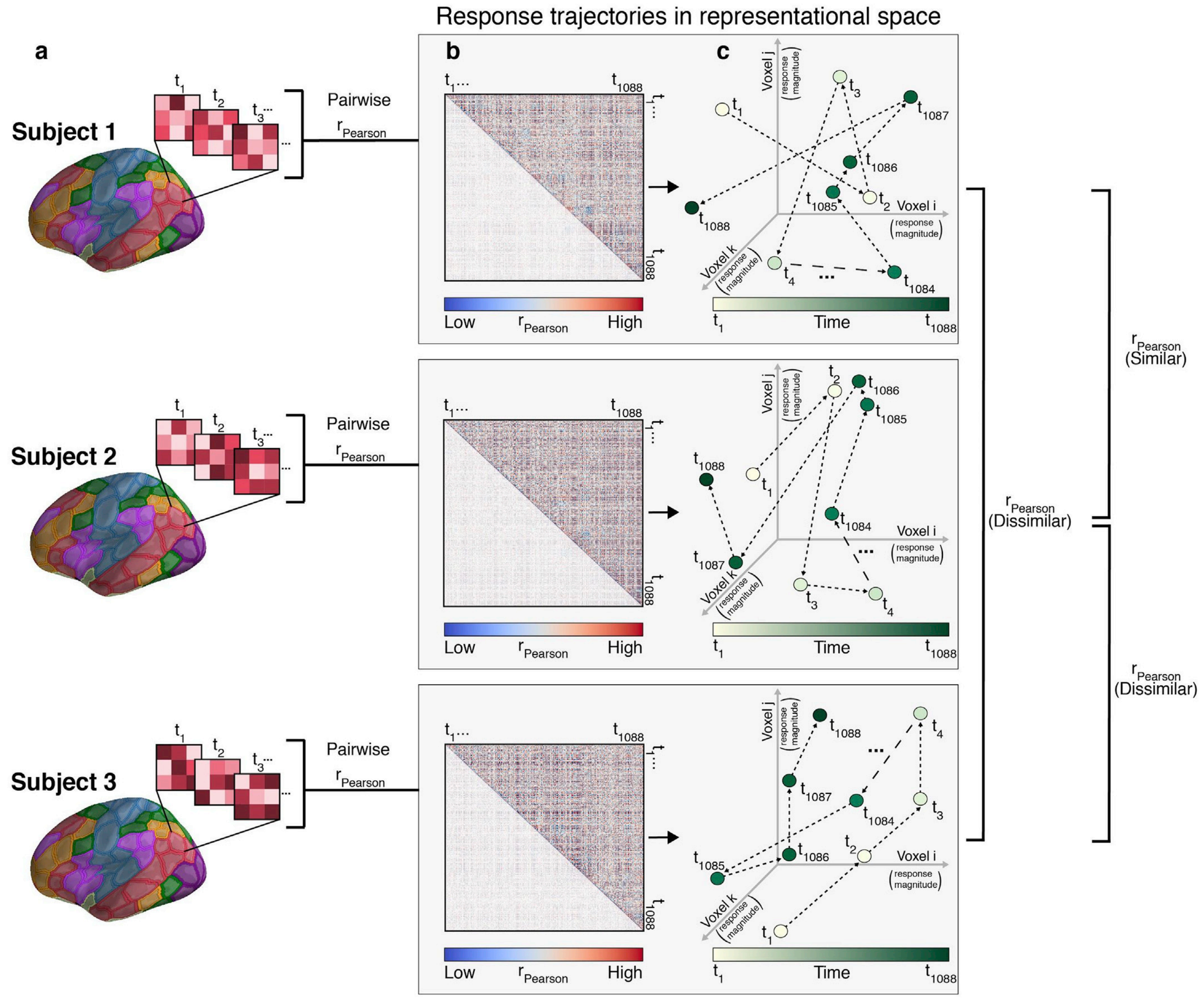

Fig. 2. Schematic illustrating the analysis of inter-subject similarity in temporal trajectories of multi-voxel patterns. (a) Subjects' data were resampled to standard space and parcellated into 200 regions of interest (ROIs) using the Schaefer et al. (2018) parcellation scheme. Each ROI is associated with a brain network from the Yeo et al. (2011) seven-network parcellation, signified by different colors. For each parcel, the multi-voxel response pattern to the stimulus was extracted at each time point. This was repeated for each subject. **(b)** Pairwise correlations between multi-voxel response patterns across time points ($n = 1088$ TRs) were calculated to generate a TR x TR matrix ("pattern trajectory matrix"). Each element of the pattern trajectory matrix reflects the degree to which multi-voxel patterns are correlated across two time points. **(c)** Multi-voxel patterns are visualized as points in a multidimensional representational space, in which each dimension reflects the response magnitude of a given voxel and the number of dimensions corresponds to the number of voxels in this brain region; color corresponds to TR order. The dotted lines connect temporally adjacent patterns. Points depicted as closer together in space reflect multi-voxel patterns that are highly correlated, relative to points that are farther apart in space. For example, Subject 1's multi-voxel patterns at TR 2, TR 1085, and TR 1086 are highly similar to each other, relative to the multi-voxel patterns at TR 1, TR 2, and TR 3. We compared the relative locations of all points in representational space (i.e., the representational geometry) between subjects by calculating Pearson correlations between the off-diagonal halves of subjects' pattern trajectory matrices. Note that coordinates in **(c)** do not reflect the actual data and are schematics provided for illustrative purposes. Cortical surface visualizations for all figures were created using PySurfer (Waskom, 2018).

(3) temporally distal trajectory structures. Given that our dataset includes 42 fMRI subjects, there were 861 unique dyads of fMRI subjects. In analysis (1), for each of the 861 dyads, we calculated the Pearson correlation between subjects' vectorized full pattern trajectory structures, and then Fisher z-transformed these values. This process yielded a measure reflecting inter-subject similarity in the trajectory of multi-voxel response patterns across the whole study.

A small number of outliers were detected in the dataset; outliers were defined as values more than 1.5 interquartile ranges (IQRs) below the first quartile or above the third quartile. Disproportionately high temporal trajectory similarity values were recoded to a value equal to the 75th percentile (i.e., upper quartile) plus 1.5 times the IQR. Disproportionately low temporal trajectory similarity values were recoded to a value equal to the 25th percentile (i.e., lower quartile) minus 1.5 times the IQR. For all analyses, results in the main text are reported after having recoded outliers; the pattern of results observed without recoding outliers was similar and is illustrated in the Supplementary Material (Figs. S1-S3). The temporal trajectory similarity values were then normalized using Scikit-learn's RobustScaler() function (Pedregosa et al., 2011). Next, to account for demographic similarities that may be related

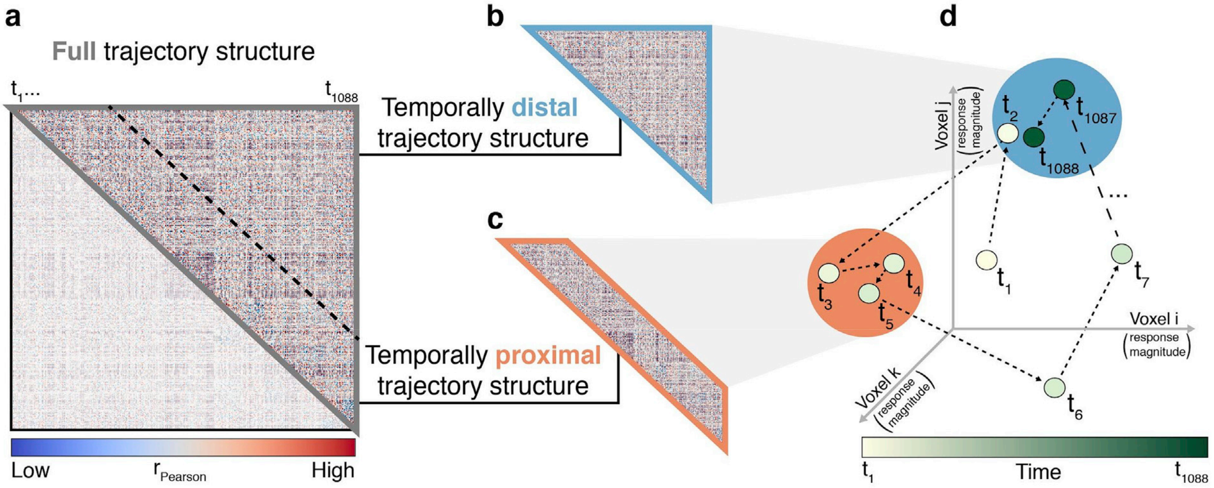

Fig. 3. Definition of distal and temporally proximal trajectory structures. (a) The whole off-diagonal half of the temporal trajectory matrix (gray outline) is defined as the full pattern trajectory structure, which contains pairwise correlations between multi-voxel response patterns between all TRs. The dashed line represents the diagonal-split that best minimizes the differences in areas between the component structures above and below it. **(b)** The resulting structure (blue outline) above the diagonal-split is defined as the temporally distal pattern trajectory structure, in which elements reflect pairwise correlations between multi-voxel patterns that occur at distant points in time. **(c)** The resulting structure (orange outline) below the diagonal-split is defined as the temporally proximal pattern trajectory structure, in which elements reflect pairwise correlations between multi-voxel patterns that occur at proximal points in time. **(d)** Multi-voxel patterns can be represented as points in a multidimensional representational space where the number of dimensions corresponds to the number of voxels in a given brain region. One example of a temporally distal trajectory is shown in the blue shaded circle. A particular multi-voxel pattern at time t_2 is highly similar to multi-voxel patterns at time t_{1087} and time t_{1088}, suggesting that a relatively similar state re-appeared across distant points in time. In the orange circle, multi-voxel patterns at time t_3, t_4, and t_5 are highly similar, suggesting that a relatively similar psychological state persisted across proximal points in time.

to social network proximity and/or neural responding, prior to all subsequent analyses, we regressed out the effects of inter-subject similarities in age, gender, ethnicity, nationality, and handedness (referred to subsequently as “control variables”) from inter-subject similarities in pattern trajectory structures.

Using OLS regression, we then tested whether dyadic similarities in full pattern trajectory structures were predictive of social network proximity, after having controlled for the effects of control variables in the previous data analytic step. These models’ true β-values were tested against null distributions of β-values generated by permutation testing. More specifically, fMRI subjects’ social network positions were randomly shuffled 1000 times, while holding all else in the dataset constant. In each permutation of the dataset, the procedure described above was repeated in order to generate a null distribution of 1000 β-values. *P*-values were derived by calculating the frequency with which the true model’s β-value exceeded the β-values in the null distribution. This procedure accounts for dependence structure of the data. In addition, to correct for having performed this procedure repeatedly across 200 brain parcels, we employed false discovery rate (FDR) correction.

These steps were repeated for analyses (2) and (3) using temporally proximal trajectory structures and temporally distal trajectory structures, respectively (i.e., instead of using the full pattern trajectory structure, which was used in analysis (1)).

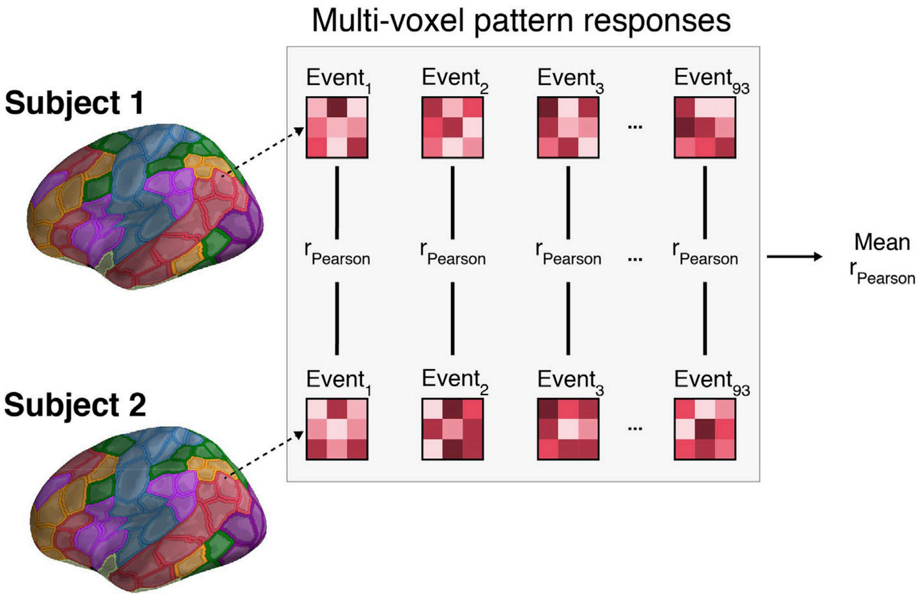

Fig. 4. Schematic illustrating the analysis of inter-subject similarity in multi-voxel patterns. When examining inter-subject similarity in multi-voxel response patterns themselves, rather than in trajectories of multi-voxel response patterns, the following analysis was performed: Stimuli were manually divided into 93 discrete events as described in Section 2.9. Multi-voxel patterns were then averaged across time points within each event, resulting in 93 “event patterns” for each parcel. This was repeated for each subject. Inter-subject correlations in corresponding event patterns for each dyad were then calculated, resulting in 93 similarity values (one for each event). These similarities were then averaged across events to yield a single mean correlation value characterizing inter-subject similarity in multi-voxel patterns for a given dyad for each parcel.

2.9. *Inter-subject similarity of multi-voxel response patterns to corresponding manually defined events*

In addition to examining inter-subject similarity in the temporal trajectories of subjects' multi-voxel response patterns, we also examined inter-subject similarity in subjects' multi-voxel response patterns themselves. An independent coder who had not participated in the experiment identified timestamps that separated the sequence of video clips into 93 different scenes ("events"). Timestamps were identified at points of major shifts in the narrative, such as changes in location, topic, and/or time (J. Chen et al., 2017; Zadbood et al., 2017). The events ranged from 8 to 60 s ($M = 23.4$, $SD = 11.9$) in duration. In each of the 200 parcels, the following analysis was performed. For each subject, we extracted the multi-voxel response patterns at each TR. Multi-voxel response patterns were then averaged across TRs within each of the 93 events, resulting in 93 multi-voxel patterns for each subject ("event patterns"). For each of the 861 dyads, we calculated Pearson correlations between subjects' multi-voxel response patterns corresponding to the same events (Fig. 4). Correlation coefficients were then Fisher z-transformed and averaged across events for each dyad, resulting in a single inter-subject multi-voxel response pattern similarity measure for each dyad for each brain parcel.

We then performed outlier recoding and data scaling as described in Section 2.8. In addition, as in Section 2.8, to account for demographic similarities, we regressed out inter-subject similarities in control variables from inter-subject similarities in multi-voxel response patterns prior to our main analyses. We then performed OLS regression and permutation-based significance testing as described in Section 2.8 in order to test if and where inter-subject similarities in multi-voxel response patterns to the same events were predictive of social network proximity.

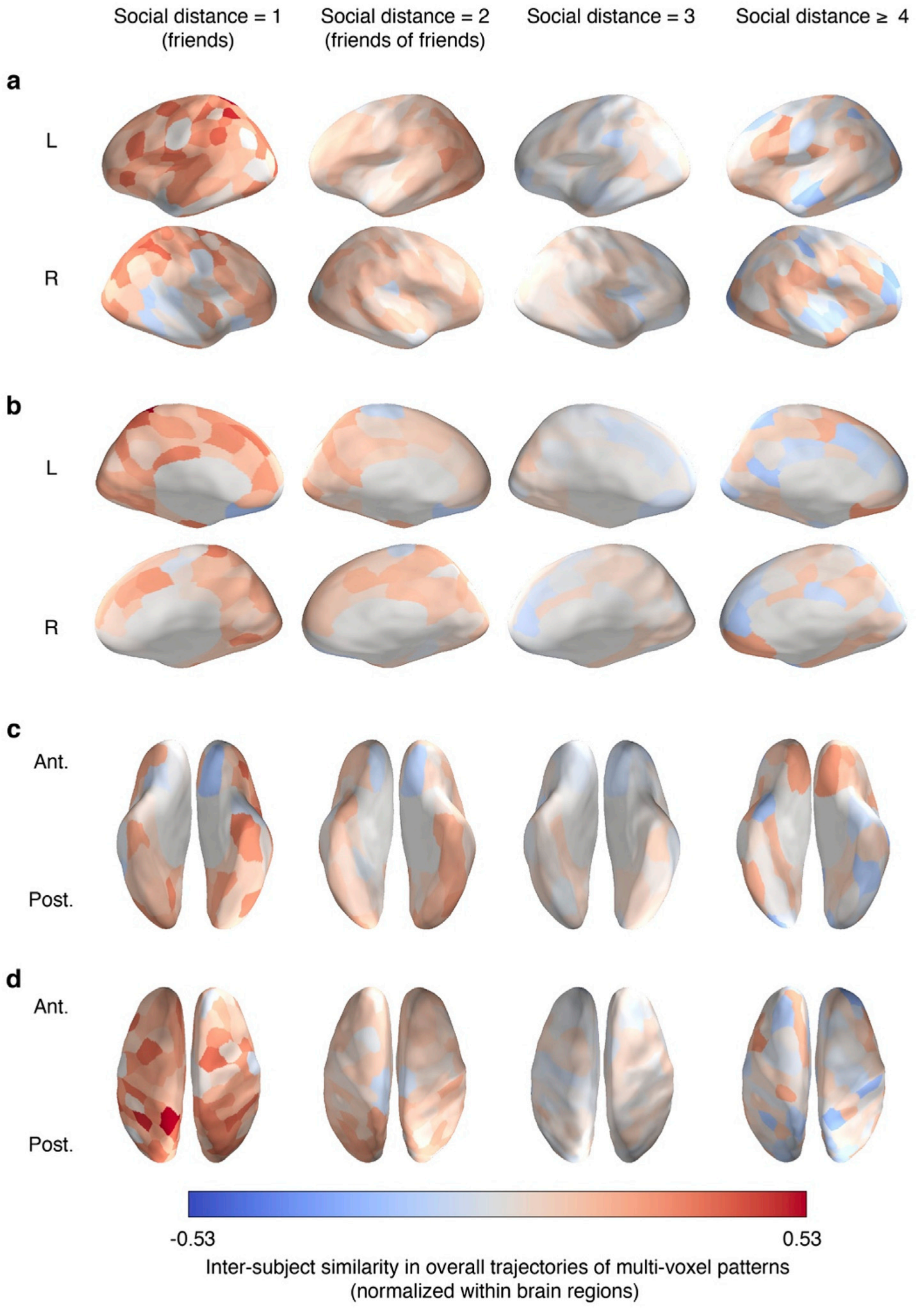

Fig. 5. Inter-subject similarities in full multi-voxel pattern trajectory structures, averaged within levels of social distance. Data are overlaid on a cortical surface model and are shown in **(a)** lateral, **(b)** medial, **(c)** ventral, and **(d)** dorsal views. To illustrate how relative similarities of overall temporal trajectories of multi-voxel response patterns varied as a function of social distance, after controlling for similarities in age, gender, nationality, ethnicity, and handedness, inter-subject neural similarities were normalized (i.e. z-scored across dyads for each region), averaged within social distance level, then projected onto an inflated model of the cortical surface. Warmer colors correspond to relatively similar pattern trajectory structures for a given region, and cooler colors correspond to relatively dissimilar pattern trajectory structures for a given region. Ant. = anterior; Post. = posterior; L = left; R = right.

2.10. Inter-subject similarity of multi-voxel response patterns to corresponding TRs

As an exploratory analysis, we also examined inter-subject similarity in subjects' multi-voxel response patterns for each TR, rather than for each event. The data analytic procedure used for this exploratory analysis was identical to that described in Section 2.9, but multi-voxel response patterns were not averaged across TRs within event boundaries. Rather, for each dyad, within each parcel, the Pearson correlation between subjects' multi-voxel response patterns corresponding to the same TR was calculated; these values were then Fisher z-transformed and averaged across TRs.

3. Results

3.1. Relating social network proximity and similarity in the temporal trajectory of multi-voxel patterns

We first examined the relationship between social network proximity and trajectories of multi-voxel response patterns throughout the entire study. Inter-subject similarities in trajectories of multi-voxel patterns for all brain regions, averaged across dyads within each level of social distance, are illustrated in Fig. 5. We note that for all analyses testing for relationships between social network proximity and neural response similarity, the effects of control variables (e.g., inter-subject similarities in terms of demographic variables and handedness) were first regressed out of relevant inter-subject neural similarity values (here, inter-subject similarities in the full trajectory structures), and the residuals were used for subsequent analyses.

Inter-subject similarity in full trajectory structures (i.e., trajectories of multi-voxel patterns across the entire study) was significantly predictive of social network proximity, above and beyond the effects of control variables, in two parcels of the left SPL that comprise part of the dorsal attention network. One such parcel, shown in Fig. 6a and b, was located in the superior aspect of the left SPL ($\beta = 0.236$; SE = 0.036; $p = 9.26 \times 10^{-11}$), and the other was located in the inferior aspect of the left SPL ($\beta = 0.218$; SE = 0.036; $p = 1.18 \times 10^{-9}$), shown in Fig. 6e and f. The relationships between social network proximity and response trajectory similarity (after having accounted for the effects of control variables) for these two parcels are illustrated in the left panels of Fig. 6c and g.

Because each fMRI subject is involved in multiple dyads, there are dyadic dependencies in the dataset. Failing to account for the non-independence of relational data of this sort can underestimate sample variability and thus yield spurious results (Croft et al., 2011). Thus, to more conservatively test our hypotheses, we employed a form of permutation testing in which the fMRI subjects' social network positions were randomly shuffled 1000 times, while holding all else constant. This procedure yielded 1000 permuted datasets that retain the overall topological structure of the social network and thus have the same dependence structure as the true dataset. As described in Section 2.8, within each permuted dataset, the OLS regression described above was performed, thus generating a null distribution of β-values against which we

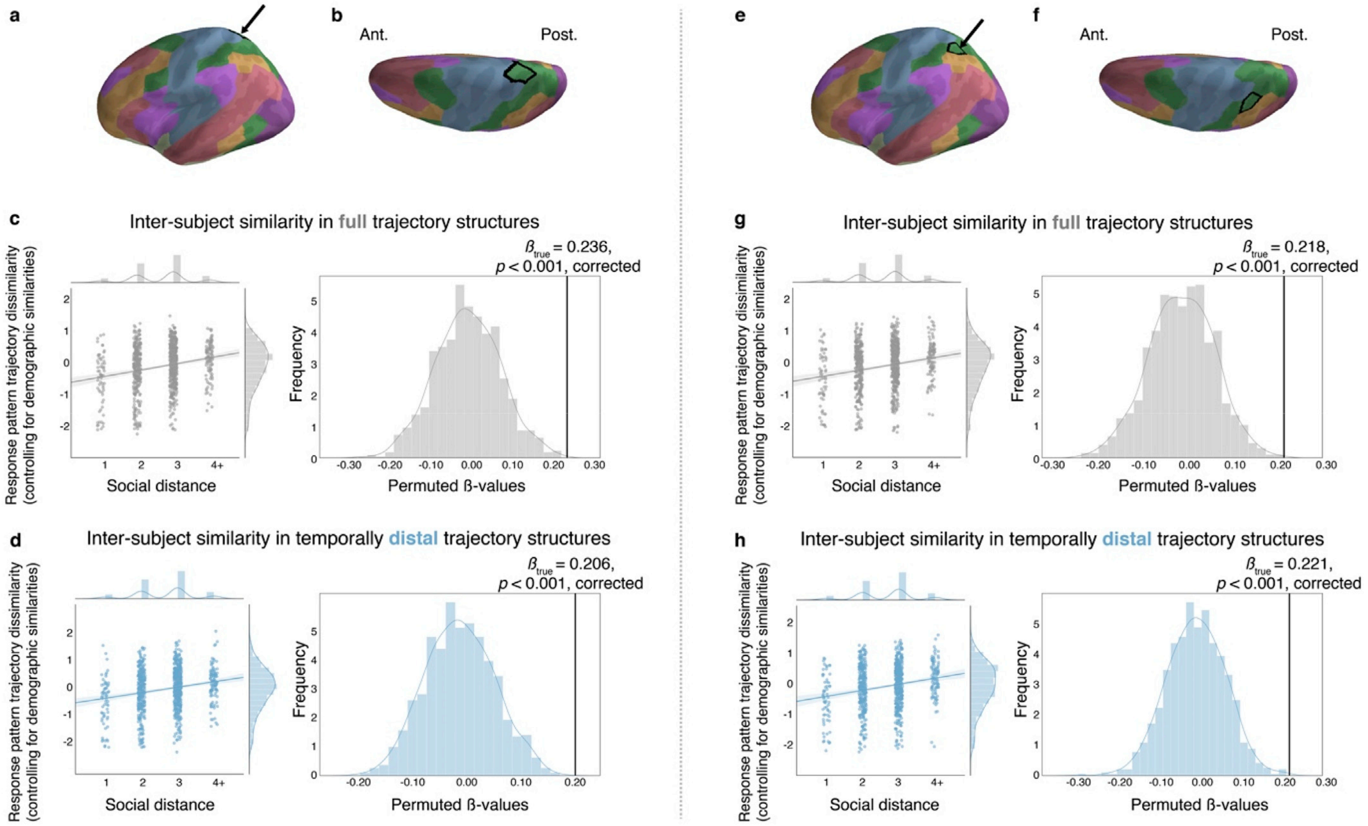

Fig. 6. Social network proximity was positively associated with inter-subject similarity in multi-voxel pattern trajectories in two regions of superior parietal cortex. The two brain regions where social network proximity was associated with similar temporal trajectories of multi-voxel response patterns are outlined in black on an inflated cortical surface, shown in lateral **(a, e)** and dorsal **(b, f)** views. **(c, g)** Scatter plots depict the positive relationship between social network proximity and multi-voxel pattern trajectory similarity for each parcel. This relationship was significant after permutation testing to account for the dependence structure of the data (see histograms in right panels of **(c)** and **(g)**) and after FDR-correction across all tested brain regions ($p < .001$, corrected). Similar results from analyses using the temporally distal trajectory structures (rather than the full pattern trajectory structures) are depicted in panels **(d)** and **(h)**. Ant. = anterior; Post. = posterior.

can compare the model that had been fit to the true data (as shown in the right panels of Fig. 6c and g) to generate an exact *p*-value. This *p*-value reflects the possibility that the relationship between social network proximity and inter-subject temporal trajectory similarity in the true dataset is greater than chance, after having accounted for the dependence structure of the data (as well as inter-subject similarities in control variables, as described above). For both SPL parcels described above, the true model's β-value was significantly greater than the permuted β-values ($p < .001$) and remained statistically significant after implementing FDR-correction to correct for multiple comparisons across all 200 brain parcels ($p < .001$, corrected), as illustrated in the right panels of Fig. 6c and g.

Regression coefficients for all parcels are depicted overlaid on the cortical surface (Fig. 7a–d) and organized by brain network (Fig. 7e). As can be seen in Fig. 7e, the direction of the relationship between social network proximity and neural response pattern trajectories was consistently positive (e.g., in nearly all parcels of the dorsal attention, visual, default mode, ventral attention, and frontoparietal task control networks). However, after accounting for the dependence structure of the data (via permutation testing) and multiple comparisons across brain parcels (via FDR correction), this relationship was only significant in two parcels located in superior posterior parietal cortex, as indicated in Fig. 7e and as illustrated in greater detail in Fig. 6.

After examining the full pattern trajectory structures, we next separately considered inter-subject similarity in *temporally proximal trajectory structures* (i.e., trajectories of multi-voxel response patterns across closely spaced time points) and in *temporally distal trajectory structures* (i.e., the trajectories of multi-voxel response patterns across distantly spaced time points). The same data analytic procedures that had been used to test the relationship between social network proximity and response pattern trajectory similarities across the full experiment were repeated when analyzing the distal and proximal trajectory structures separately.

Inter-subject similarities in distal trajectory structures for all brain regions, averaged within each level of social distance, are illustrated in Fig. 8. Social network proximity was positively related to similarity of distal trajectory structures in two parcels located in superior parietal cortex (the same two parcels that were implicated in analyses of the full trajectory structures; see Fig. 6d and h). Similar to the pattern of results that was observed when using the full trajectory structures, the direction of the relationship between social network proximity and neural pattern trajectory similarity across distal time points was positive in both the superior ($\beta = 0.206$; SE $= 0.034$; $p = 1.67 \times 10^{-9}$) and inferior ($\beta = 0.221$; SE $= 0.035$; $p = 7.56 \times 10^{-10}$) parcels of superior parietal cortex in which a significant relationship was observed. Again, both of these

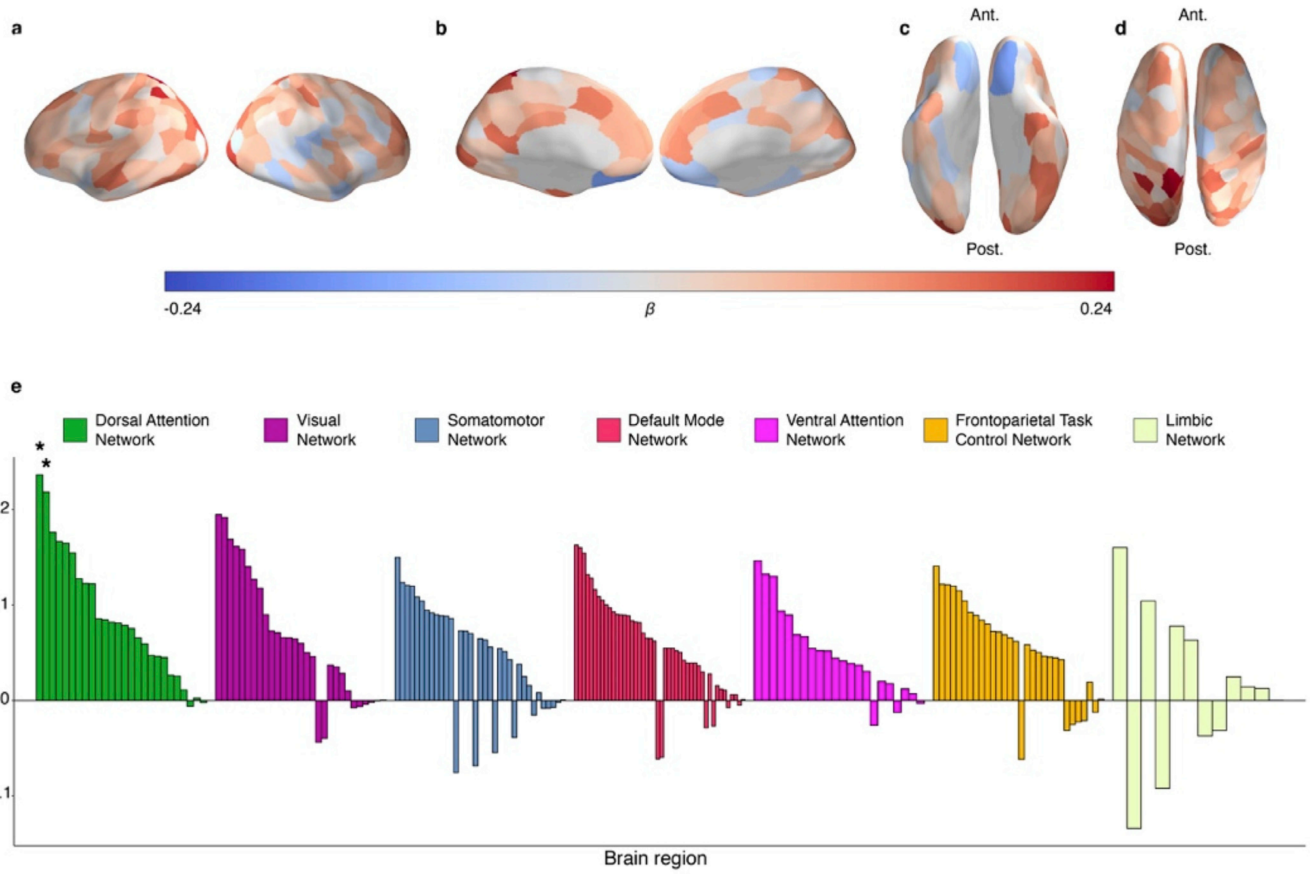

Fig. 7. Relationships between inter-subject similarity in multi-voxel pattern trajectories across the full study and social network proximity for all brain regions. For each brain parcel, OLS regression was performed to model social network proximity as a function of dyadic similarity in the trajectory of multi-voxel patterns across all time points (i.e., full pattern trajectory structures), after having accounted for control variables (e.g., demographic similarities). Regression coefficients for each parcel are shown overlaid on **(a)** lateral, **(b)** medial, **(c)** ventral, and **(d)** dorsal views of the inflated cortical surface. Warmer colors correspond to positive regression coefficients (i.e., where the direction of the relationship between social network proximity and similarity of multi-voxel pattern trajectories was positive). Cooler colors correspond to negative regression coefficients (i.e., where the direction of the relationship between social network proximity and similarity of multi-voxel pattern trajectories was negative). **(e)** The same regression coefficients for each of the brain parcels are shown, grouped by their associated brain networks. Brain parcels in which neural similarity was significantly associated with social network proximity are marked by asterisks ($p < .001$, FDR-corrected, two-tailed). Ant. = anterior; Post. = posterior.

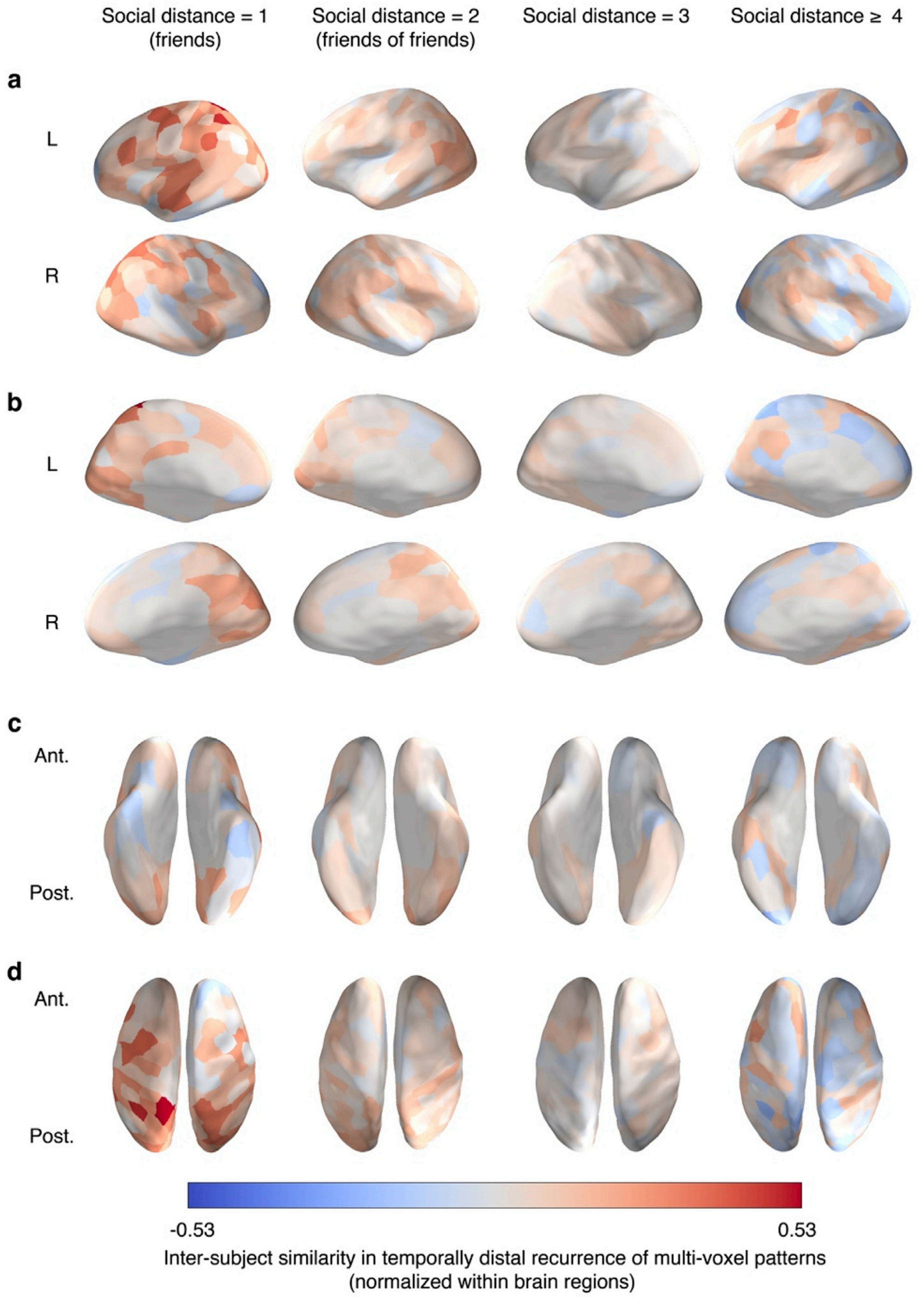

Fig. 8. Inter-subject similarities in temporally distal pattern trajectory structures, averaged within levels of social distance. Data are projected onto a cortical surface model and are shown in **(a)** lateral, **(b)** medial, **(c)** ventral, and **(d)** dorsal views. To illustrate how relative similarities of long-range temporal trajectories of multi-voxel response patterns varied as a function of social distance, after controlling for similarities in age, gender, nationality, ethnicity, and handedness, inter-subject neural similarities were normalized (i.e., z-scored across dyads for each region), averaged within social distance level, then visualized on an inflated model of the cortical surface. Warmer colors correspond to relatively similar distal trajectory structures for a given region, and cooler colors correspond to relatively dissimilar distal trajectory structures for a given region. Ant. = anterior; Post. = posterior; L = left; R = right.

parcels were significant after applying permutation tests to account for the dependence structure of the data ($p < .001$ for both parcels; as shown in the right panels of Fig. 6d and h), and after FDR-correction across the 200 parcels ($p < .001$, corrected).

Regression coefficients for all parcels from analyses of the distal trajectory structures are depicted on the cortical surface in Fig. 9a–d and organized by brain network in Fig. 9e. Similar to the results that were observed when using the full trajectory structures, there was a positive relationship between the similarity of neural response pattern trajectories across distal time points and social network proximity in the vast majority of parcels within the dorsal attention and visual networks. However, this was true to a lesser extent than it had been when examining the full trajectory structure in other networks, such as the default mode, ventral attention, and frontoparietal control networks (Fig. 9e). As with the analyses using the full trajectory structures, after accounting for the dependence structure of the data (via permutation testing) and multiple comparisons across brain parcels (via FDR correction), the relationship between similarities in participants' distal trajectory structures and their social network proximity was only significant in two parcels located in superior posterior parietal cortex (as shown in Figs. 9e and 6d and 6h).

In contrast to the results of analyses using the full trajectory structures and the distal trajectory structures, no significant relationship was observed between inter-subject similarity in proximal trajectory structures (i.e., the trajectory of multi-voxel patterns across points that were close in time) and social network proximity.

As described above, the boundary between the distal and proximal trajectory structures was selected such that the resultant matrices would be equal in size. That said, this boundary is relatively arbitrary, as it is based on the duration of the study. As such, we performed a set of

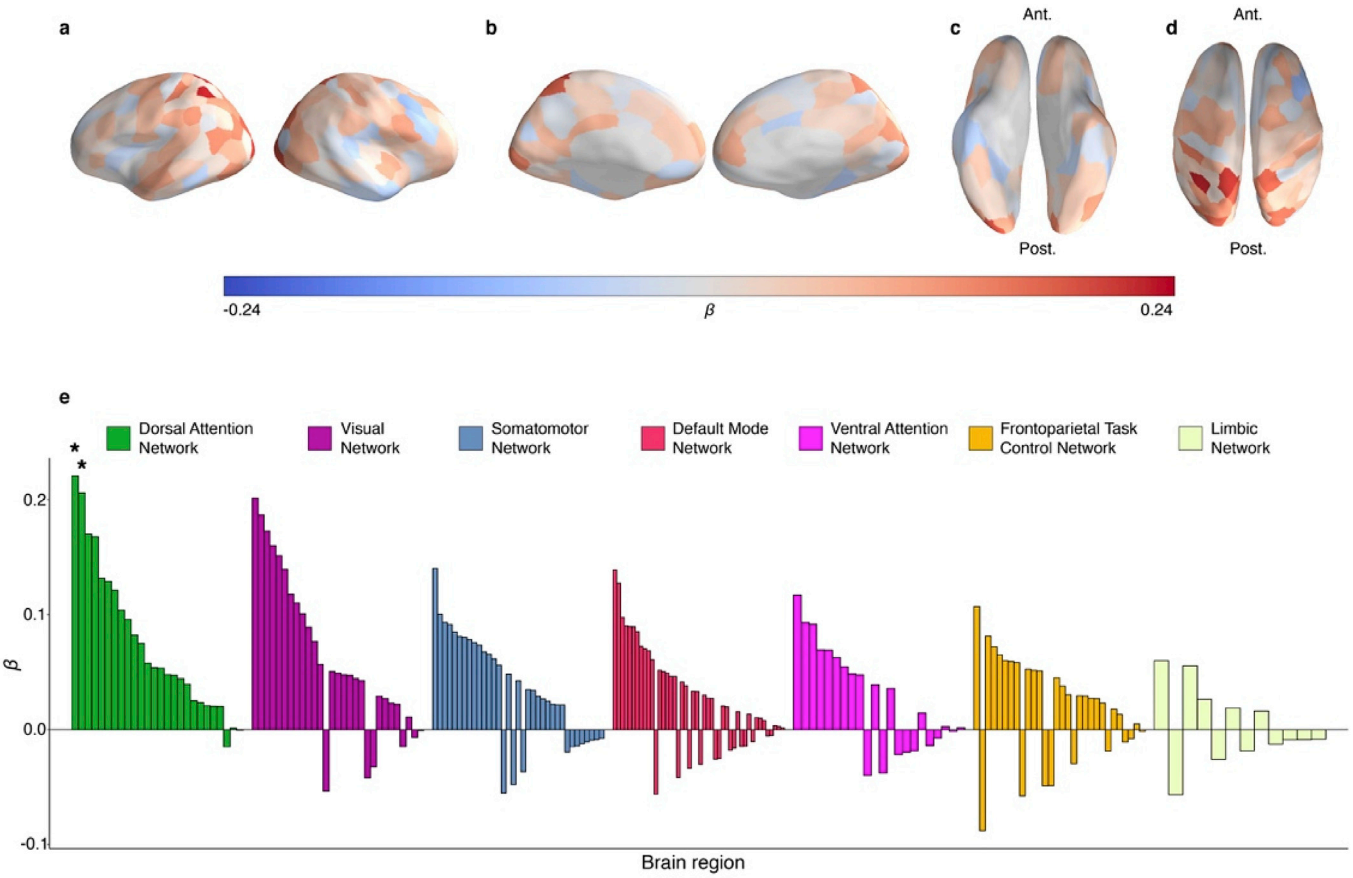

Fig. 9. Relationships between inter-subject similarity in multi-voxel pattern trajectories across distant time points and social network proximity for all brain regions. For each parcel, OLS regression was performed to model social network proximity as a function of dyadic similarity in trajectories of multi-voxel patterns across distant time points (i.e., temporally distal trajectory structures), after accounting for control variables (e.g., demographic similarities). Regression coefficients for each parcel are shown overlaid on **(a)** lateral, **(b)** medial, **(c)** ventral, and **(d)** dorsal views of the inflated cortical surface. Warmer colors correspond to positive regression coefficients (i.e., where the direction of the relationship between social network proximity and temporally distal trajectory structure similarity was positive). Cooler colors correspond to negative regression coefficients (i.e., where the direction of the relationship between social network proximity and distal temporally distal structure similarity was negative). **(e)** The same regression coefficients for each of the brain parcels are shown, grouped by their associated brain networks. Brain parcels where neural similarity was significantly associated with social network proximity are marked by asterisks ($p < .001$, FDR-corrected, two-tailed). Ant. = anterior; Post. = posterior.

complementary secondary analyses involving a data-driven approach to dividing full trajectory structures into component structures that approximately map onto the proximal and distal trajectory structures defined in our main analysis (as described in more detail in the Supplementary Material and as illustrated in Fig. 10). Briefly, we used modified Hidden Markov Models (HMMs) to divide the temporal sequences of multi-voxel response patterns into a smaller number of contiguous, stable activity patterns (i.e., to perform event segmentation, Baldassano et al., 2017). This approach was used to determine whether a given pair of TRs should be treated as "within-event" (i.e. if both TRs are in the same event) or "between-events" (i.e., if the TRs are in separate events). Conceptually, this within-event vs. between-events distinction approximately mirrors our distinction between temporally proximal and distal trajectory structures. We observed a pattern of results similar to those of our main analyses when conducting analyses using the HMM-defined within-event and between-events trajectory structures. More specifically, in the same two posterior parietal regions where social network proximity was positively related to inter-subject similarity in distal, but not proximal, trajectory structures, social network proximity was also positively related to inter-subject similarity in multi-voxel pattern trajectory structures that captured how multi-voxel patterns changed between, but not within, events ($p < .001$, corrected). For further details of these analyses and results, please see the Supplementary Material.

Additionally, given that inter-subject similarity in both the full and distal trajectory structures was associated with social network proximity in our main analyses, we performed subsequent analyses testing if the relationship between social network proximity and inter-subject similarity in multi-voxel pattern trajectory structures across the entire experiment was driven by the distal component of the full trajectory structure. More specifically, we controlled for inter-subject similarity in distal trajectory structures when testing whether inter-subject similarity in full trajectory structures was predictive of social network proximity. After controlling for inter-subject similarity in the trajectories of multi-voxel response patterns across distant points in time (i.e., in the distal trajectory structures), inter-subject similarity in the full trajectory structures was no longer significantly associated with social network proximity, suggesting that inter-subject similarity in the distal trajectory structures was driving the observed relationship between social network proximity and inter-subject similarity in full pattern trajectory structures.

Given that the majority of previous research on inter-subject similarities in neural responses to naturalistic stimuli has focused on similarities in how the overall magnitude of local neural responses change over time (rather than on similarities in how multi-voxel response patterns change over time), we also conducted secondary analyses focused

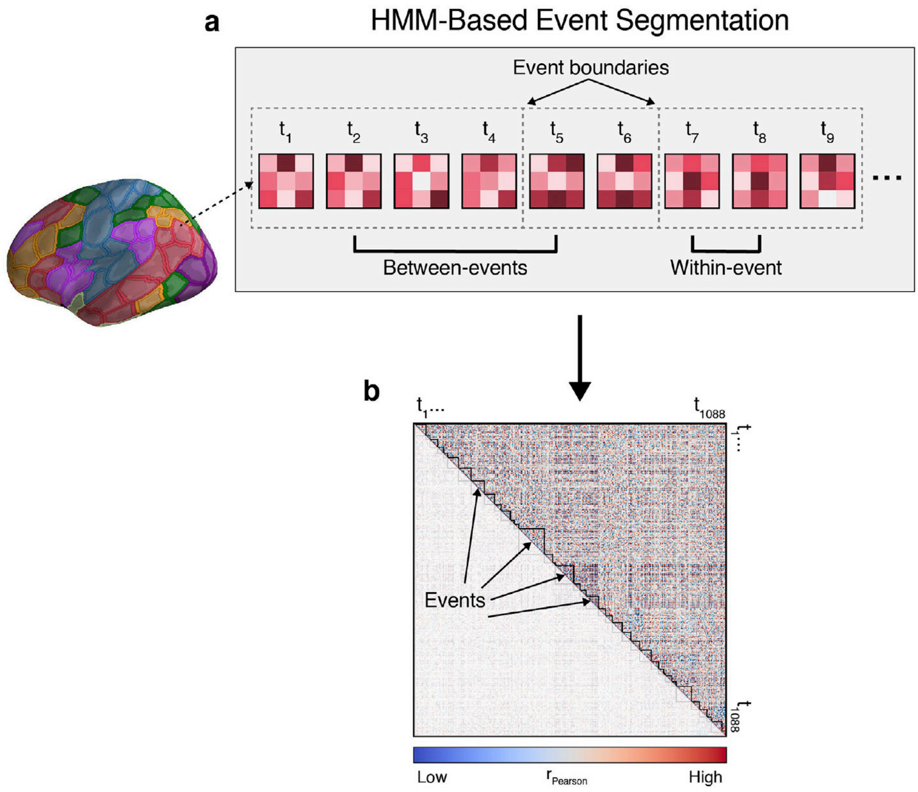

Fig. 10. Using data-driven event segmentation to divide full pattern trajectory structures into component structures. (a) In a given parcel, a modified Hidden Markov Model is applied to the multi-voxel time course to identify temporally contiguous events that reflect latent "states" characterized by relatively stable patterns of multi-voxel responses. These events are separated by event boundaries, which are characterized by rapid shifts in multi-voxel response patterns. A pair of multi-voxel patterns within an event is characterized as being "within-event," and a pair of multi-voxel patterns in different events is characterized as being "between-events." **(b)** Correlations between multi-voxel patterns that are within-event are located within the black structures located along the diagonal of the pattern trajectory structure (i.e., between the diagonal and the black outlines along the diagonal). Correlations between multi-voxel patterns that are between-events are located in the rest of the pattern trajectory structure that are to the right of the events outlined in black.

on how region-averaged BOLD responses change over time (i.e., conventional temporal ISC, described in more detail in the Supplementary Material). Average inter-subject similarities in pattern trajectory structures are shown overlaid on a cortical surface model in Fig. 11a–d, alongside average inter-subject time series similarities (Fig. 11e–h). As shown in Fig. 11a–h, there appear to be differences in these two ways of characterizing inter-subject response similarities, both with respect to the magnitude and spatial distribution of results. More specifically, examining region-averaged time series produced overall higher average ISCs, with average ISCs of up to $r = 0.32$ and $r = 0.31$ in parcels located in lateral left and right posterior superior temporal cortex, respectively. In contrast, comparing subjects with respect to pattern trajectories produced relatively lower ISCs, with average ISCs of up to only $r = 0.11$; the greatest similarities across-subjects observed using this method were in left and right anterior inferior temporal cortex.

In addition, given that prior work has found inter-subject similarity in region-averaged response magnitude fluctuations to be positively related to social network proximity (Parkinson et al., 2018), we repeated our main analyses keeping all aspects of the data analytic procedure constant, but using subjects' response magnitude fluctuations, rather than their pattern trajectory structures, to characterize neural responding. The regression coefficients for all parcels from analyses relating these inter-subject similarities in response magnitude fluctuations to social network proximity are illustrated in Fig. 11m-p, and are displayed alongside the regression coefficients from analyses based on pattern trajectory structures (i.e., from our primary analyses, Fig. 11i-l) for ease of visual comparison. The results of these analyses are discussed in more detail in the Supplementary Material. To more directly test if inter-subject similarity in multi-voxel pattern trajectories was associated with our outcome of interest in the current study (i.e., social network proximity), beyond what might be found if only characterizing neural responses in terms of response magnitude fluctuations, we tested if the relationships between inter-subject similarity in pattern trajectory structures and social network proximity (Fig. 6) observed in our main analyses would persist after controlling for inter-subject similarity in temporal ISC. When doing so, inter-subject similarity in both the full and temporally distal trajectory structures remained predictive of social network proximity in both the superior ($\beta = 0.160$; SE $= 0.036$) and inferior ($\beta = 0.138$; SE $= 0.035$) aspects of the SPL implicated in our main analyses ($p < .001$ for both parcels). Taken together, these results suggest that multi-voxel pattern trajectory structures may capture facets of inter-individual differences in neural responding that are not accounted for by region-averaged response magnitude fluctuations (i.e., by conventional temporal ISC), and that these aspects of inter-individual differences in neural responding are distinctively related to socio-behavioral outcomes (e.g., social network proximity).

The results of additional exploratory analyses using alternative ways of defining the trajectory structures (e.g., alternative distance measures, comparing patterns by event rather than by TR) and ways of defining the social network are provided in the Supplementary Material.

3.2. *Relating social network proximity and multi-voxel pattern similarity*

In addition to assessing whether friends share similarities in trajectories of multi-voxel response patterns, we also investigated whether friends share similarities in multi-voxel response patterns themselves. Following previous work that has demonstrated above-chance inter-subject similarity in multi-voxel response patterns to discrete events within a naturalistic audiovisual stimulus (J. Chen et al., 2017; Zadbood et al., 2017), our stimuli were manually divided into discrete events as described in Section 2.9. This allowed us to characterize each dyad in terms of the similarity of their spatial response pattern, within each parcel, to each manually defined event. As described in Section 2.9, we then obtained interpersonal similarities in spatial response patterns for each dyad, within each parcel, averaged across events, and used OLS regression to assess the relationship between social network proximity

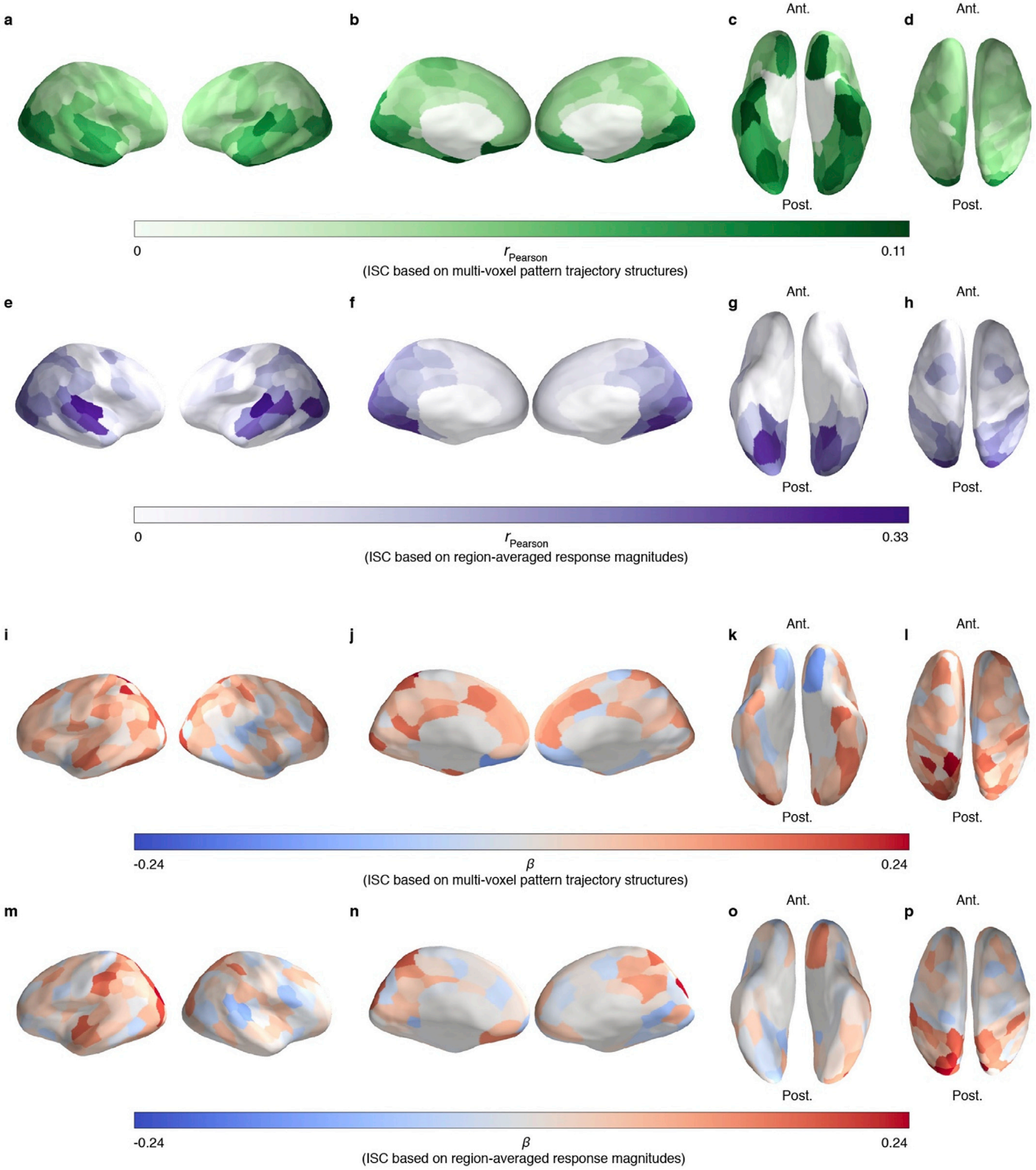

Fig. 11. Comparing trajectories of multi-voxel response patterns and of region-averaged response magnitudes: Overall inter-subject similarities and relationships with social network proximity. Average inter-subject similarities in pattern trajectory structures across all dyads are shown overlaid on an inflated cortical surface model in lateral **(a)**, medial **(b)**, ventral **(c)**, and dorsal **(d)** views, alongside average inter-subject similarities in region-averaged response time series **(e-h)**. In the top two rows **(a-h)**, darker colors correspond to higher inter-subject similarity. For each parcel, OLS regression was performed to test the relationship between social network proximity and response pattern trajectory structures, after accounting for control variables. Regression coefficients for each parcel are overlaid on inflated cortical surfaces in **i-l** (these coefficients are also depicted in Fig. 7a–d and are provided here for ease of visual comparison between the results using these two methods). Regression coefficients from analogous analyses based on region-averaged time courses are displayed in **m-p**. In the bottom two rows **(i-p)**, warmer colors correspond to positive regression coefficients (i.e., where the direction of the relationship between social network proximity and neural similarity was positive), and cooler colors correspond to negative regression coefficients (i.e., where the direction of the relationship between social network proximity and neural similarity was negative). Ant. = anterior; Post. = Posterior.

and inter-subject similarity in multi-voxel response patterns to corresponding events. No significant relationship was observed between social network proximity and similarities in multi-voxel response patterns, averaged across events, in any of the 200 brain parcels.

We also conducted an additional exploratory analysis, as described in Section 2.10, in which we tested whether inter-subject similarity in multi-voxel response patterns to corresponding TRs (rather than to corresponding events, aggregated across TRs) would be associated with social network proximity. Social network proximity was significantly positively associated with inter-subject similarity in multi-voxel response patterns in a single parcel located in early visual cortex (Fig. S4a-c), $\beta = 0.194$; $SE = 0.035$; $p = 4.01 \times 10^{-8}$. This effect remained significant after permutation testing (Fig. S4) to account for the dependence structure of the data and survived FDR-correction ($p < .001$, FDR-corrected). Regression coefficients for this exploratory analysis for all parcels are illustrated in Fig. S5. Unlike the pattern of results that was observed when analyzing inter-subject similarities of multi-voxel pattern *trajectories* (Fig. 7; Fig. 11), when examining multi-voxel patterns *themselves* (Fig. S5), there was not a consistently positive relationship between social network proximity and inter-subject neural similarity across brain parcels overall, or across parcels within any brain network. This can also be seen in Fig. S6, in which inter-subject similarities of multi-voxel response patterns are shown for all parcels, averaged across dyads within each level of social distance.

Thus, whereas *trajectories* of multi-voxel response patterns evoked by naturalistic stimuli are similar among people who are closer in social ties, particularly in regions of the dorsal attention network (Fig. 7; Fig. 9), similarity in multi-voxel response patterns *themselves* seems to be less consistently related to social network proximity. There were no significant relationships between multi-voxel pattern similarity and social network proximity in any brain regions in our planned analyses (in which spatial response patterns were summarized by event, consistent with prior work, Chen et al., 2017; Zadbood et al., 2017). In an exploratory analysis where inter-subject spatial pattern similarity was summarized by TR, rather than by event (described in Section 2.10), results were relatively heterogeneous in direction across parcels (Fig. S5) compared to results of similar analyses on pattern trajectories (Fig. 7; Fig. 9), and implicated a single parcel in early visual cortex. We note that this result should be interpreted with some caution, given that this parcel was not significant in our planned analyses relating spatial pattern similarity and social network proximity (which yielded no significant results).

4. Discussion

We found that people who are closer together in social ties have more similar trajectories of multi-voxel response patterns during naturalistic stimulation in superior parietal cortex. Whereas past research has tended to characterize responses to naturalistic stimuli in terms of overall response magnitude fluctuations, these results suggest that trajectories of spatially distributed response patterns provide an additional window into individual differences in responding to such stimuli. Further, the relationship between social network proximity and multi-voxel pattern trajectory similarity was localized to relatively high-level cortical regions (i.e., posterior superior parietal cortex) and only emerged when considering the temporal trajectories of patterns across long expanses of time (i.e., several minutes). Inter-subject similarity in trajectories of multi-voxel response patterns in these regions was predictive of social network proximity above and beyond the effects of inter-subject similarity in overall response magnitude fluctuations. Taken together, these results suggest that people closer together in the social network may be particularly similar in how aspects of their psychological states related to high-level processing and endogenous attention evolve over time during natural stimulation. More generally, they demonstrate that temporal trajectories of multi-voxel response patterns capture behaviorally relevant individual differences in neural responding that are distinct from those captured by temporal fluctuations in region-averaged BOLD responses.

Given that the superior parietal cortex has a long-standing role in top-down modulations of attention, one possibility is that social network proximity is associated with similar patterns of attentional allocation to stimuli over time. For example, the SPL directs attention within external stimuli based on a perceiver's internally-determined priorities, both with respect to spatial attention (e.g., attending to different locations within a stimulus, Molenberghs et al., 2007) and object-based attention (e.g., attending to different but spatially overlapping aspects of a stimulus; Serences et al., 2004). In the current study, similarities in multi-voxel response pattern trajectories among friends may have been related to similarly timed fluctuations in attention to various aspects of the video clips (e.g., to different points in the scenes, to different aspects of the narrative).

Another possibility pertains to shifts of attention in internal knowledge representations and memories rather than in external stimuli. In addition to their well-known role in supporting top-down attention to external stimuli, regions of the dorsal attention network, such as the SPL, are also often implicated in episodic memory retrieval, and in particular, in allocating attention to memories (Hutchinson et al., 2009). In other words, in the same way that the SPL allocates attention to external stimuli based on endogenous factors (e.g., the perceiver's current goals, what they consider relevant or interesting), this region is thought to underlie top-down shifts of internally directed attention (e.g., to memories; Cabeza et al., 2008). Thus, the results of our main analyses may reflect similarity in how socially close individuals allocated their attention to the stimuli, to their own internal states and memories, or some combination of these phenomena, while watching the video clips.

We note that significant effects were localized to regions of dorsal posterior parietal cortex that comprise part of the dorsal attention network, which is associated with endogenously-driven shifts of attention, and not, for example, to regions of the ventral attention network, which underlies exogenously-driven shifts of attention (Corbetta and Shulman, 2002). This is consistent with the fact that all participants were exposed to the same stimulus, and correspondingly, may not have differed substantially in how exogenously-determined attentional states fluctuated over time. However, the current results suggest that friends (and more generally, people in closer social proximity) are exceptionally similar in how their endogenously-driven attentional states fluctuate over time during naturalistic stimulation. This may be because friendship is associated with similarity in people's dispositional characteristics and prior experiences, which in turn produce similarity in their goals, knowledge, and expectations when perceiving stimuli, and thus, in which aspects of the stimuli (or their own memories) are deemed relevant and/or interesting at particular points in time. Of course, the SPL is a functionally heterogenous brain region, and has also been implicated in a variety of other processes, including sensorimotor integration, maintaining expectancies, and the manipulation and rearrangement of information in working memory (Koenigs et al., 2009; Kastner and Ungerleider, 2000; Wolpert et al., 1998). Thus, we cannot decisively conclude which mental processes underlie the results reported here. However, given the particularly well-established role of the SPL in endogenous shifts of attention, both in the external environment and in internal representations and memories, we suggest that the current findings are likely driven by exceptionally similar endogenously-determined trajectories of attentional states among socially close individuals. The nature of the attentional phenomena of particular relevance here (e.g., attention to different aspects of stimuli and/or to one's own memories, covert and/or overt attentional shifts) are an important direction for future research. Future studies using more constrained paradigms, behavioral measures, and complementary modalities of measurement (e.g., eye-tracking) will be useful in pinpointing the psychological phenomena underlying the results found here.

Significant relationships between social network proximity and multi-voxel pattern trajectory similarity were found when examining participants' full trajectory structures (i.e., pattern fluctuations across the entire experiment) and distal trajectory structures (i.e., pattern fluctuations across remotely space time points), but not when examining proximal trajectory structures (i.e., pattern fluctuations spaced close together in time). In addition, follow-up analyses revealed that the relationship between social network proximity and inter-subject similarity in full pattern trajectory structures was driven by inter-subject similarity in how multi-voxel response patterns differed between distant points in time. Prior research has shown that brain regions evince a hierarchy of temporal receptive windows (i.e., the relative extent to which past information is available for processing), such that early sensory areas have relatively short temporal receptive windows, whereas higher-level regions (e.g., regions of posterior parietal cortex) have relatively long temporal receptive windows, facilitating the accumulation of information and the integration of meaning that unfolds over relatively longer periods of time, up to several minutes (Hasson et al., 2008; Lerner et al., 2011). Individual differences in high-level processing of dynamic stimuli may be more readily observable in brain regions characterized by longer temporal receptive windows, and correspondingly, when focusing on distal, rather than proximal, trajectory structures.

It is important to keep in mind that the boundary between proximal and distal time points in our primary analyses did not correspond to empirically determined differences in the temporal receptive windows of particular brain regions or in the hypothesized timescales of the persistence or trajectory of particular psychological states. Rather, this distinction was established using a method that is inherently bound to the duration of the stimulus (i.e., by finding the diagonal that would minimize the difference in areas between the proximal and distal trajectory structures; Fig. 3). Given this relatively arbitrary definition of the proximal and distal trajectory structures, we performed a complementary analysis in which we applied a data-driven technique (using modified HMMs; see Fig. 10) to partition the time series of multi-voxel response patterns in a given brain region into series of events based on how multi-voxel response patterns changed over time in that region. This allowed us to partition the full trajectory structures in the two SPL parcels in which we observed significance in the main analyses into within-event (i.e., "proximal") and between-events (i.e., "distal") trajectory structures in a more data-driven manner (Supplementary Material; Fig. 10). Inter-subject similarity in between-events trajectory structures, but not in within-event trajectory structures, was predictive of social network proximity. Thus, the results of these supplementary analyses converged with those of our main analyses and further demonstrate that people closer together in social ties (e.g., friends) may share exceptionally similar fluctuations in multi-voxel patterns across relatively disparate, but not proximal, points in time.

Future work relating multi-voxel response pattern trajectories to individual difference variables could benefit from using these and other methods to partition or transform trajectory structures or to constrain analyses to particular portions of full trajectory structures. For example, recent work has shown that topological response patterns, just like response magnitudes, fluctuate at different rates at different levels of the cortical processing hierarchy (Baldassano et al., 2017). Thus, when testing for relationships between response pattern trajectories and individual difference measures (e.g., relative social network position, trait measures) in future research, it may prove useful to examine multi-voxel pattern trajectories across different temporal distances (i.e., at different frequencies) depending on the response properties of the brain region(s) of interest and/or depending on the known or hypothesized temporal dynamics of the psychological processes of interest.

The results visualized in Fig. 11 suggest that inter-subject similarities in neural responses to naturalistic stimuli based on response pattern, rather than magnitude, trajectories pick up on distinct aspects of neural processing, which in turn, may be differentially related to real-world outcomes (e.g., social network proximity). A large body of evidence from event-related fMRI studies demonstrates that changes in the psychological meaning signaled by a brain region are often carried in its relatively fine-grained, spatially distributed, response patterns, including when the extent to which that brain region is recruited overall (i.e., its response magnitude) does not change (Norman et al., 2006; Haxby et al., 2014). Thus, differing psychological states could be signaled in how multi-voxel response patterns change over time, separately from overall response magnitude fluctuations. In the same way that two psychological states may correspond to similar overall response magnitudes in a given brain region but distinct multi-voxel patterns of activity, examining trajectories of multi-voxel patterns, rather than region-averaged response magnitudes, may provide additional sensitivity to individual differences in processing. Such individual differences can be missed when considering only univariate response magnitude fluctuations. The psychological meaning associated with brain state fluctuations will, of course, differ depending on the brain region being considered. For example, in brain regions that underlie top-down allocation of attention, such as the superior parietal regions implicated in our main analyses, fluctuations in region-averaged response magnitude may reflect fluctuations in *overall levels* of attention, whereas trajectories of multi-voxel response patterns may be more related to changes in *how* attention is allocated (e.g., to different aspects of a stimulus and its meaning, to relevant memories). The fact that inter-subject similarity in multi-voxel pattern trajectories was associated with social network proximity over and above the effects of inter-subject similarity in response magnitude fluctuations in the SPL suggests that friends may be exceptionally similar in how their endogenously-driven attentional states evolve over time, which, as we discuss earlier in this section, may be due to similar information processing goals, knowledge, and expectations about the stimuli.

In addition, we note that brain regions that have been widely implicated in social cognition and representing abstract concepts (e.g., medial prefrontal cortex, anterior inferior temporal cortex; Adolphs, 2009; Wang et al., 2017) were more similar across subjects (relative to other brain regions) when characterizing participants in terms of multi-voxel response pattern trajectory structures (Fig. 11b and c) rather than in terms of response magnitude fluctuations (Fig. 11f and g). Indeed, whereas the overall highest inter-subject similarities in region-averaged response magnitude fluctuations were observed in areas associated with auditory and visual perception (Fig. 11e–h), the overall highest inter-subject similarities in pattern trajectory structures were observed in parcels in the anterior inferior temporal cortex (Fig. 11a–d). This suggests that comparing perceivers in terms of how multi-voxel response patterns change over time (rather than only in terms of response magnitude fluctuations) may be a particularly promising method for capturing inter-subject similarities in regions involved in relatively high-level processing. In those areas, multi-voxel response pattern trajectories may capture similarities in how states change over time that are not captured when only considering fluctuations in overall response magnitudes. In addition, inter-subject similarity in multi-voxel response pattern trajectories (Fig. 11i-l), but not response magnitude fluctuations (Fig. 11m-p), tended to be positively associated with social network proximity in the medial prefrontal cortex and in the vicinity of the temporal poles. However, this relationship was not significant after correcting for the dependence structure of the data and multiple comparisons across brain parcels. Therefore, while we hesitate to read too much into these particular results given that they did not meet our corrected significance threshold, we suggest that characterizing how multi-voxel response patterns evolve over time during natural stimulation may be a particularly promising method for characterizing individual differences in high-level processing and predicting sociobehavioral outcomes in future research.

The spatial pattern of results observed here is undoubtedly influenced by the choice of stimuli used and the processing demands associated with those stimuli. For example, the majority of videos depicted a single individual speaking directly to the camera (e.g., in the context of a documentary interview, a televised debate, a scientific demonstration, and an excerpt of television news; see Table S1); few depicted social interactions unfolding over time. This may be related to why some brain areas, such as the medial prefrontal cortex (implicated in observing and interpreting social interactions between other individuals; Mitchell, 2009), were not implicated in any of our main analyses. That said, whereas regions of medial prefrontal cortex did not appear to be markedly coupled between participants or to differ in coupling as a function of social distance when participants' responses were characterized in terms of overall magnitude fluctuations, inter-subject similarity in multi-voxel response pattern trajectories in medial prefrontal cortex was weakly positively associated with social network proximity (although, as noted above, this relationship was not significant using a corrected threshold), as shown in Fig. 11j. Nonetheless, the general apparent differences pertaining to this and other brain regions when comparing participants in terms of their multi-voxel response pattern trajectories (Fig. 11a–d, Fig. 11i–l) and their region-averaged response time courses (Fig. 11e–h, Fig. 11m-p) suggests that the spatial pattern of results observed here and in related research (Parkinson et al., 2018) depends critically not only on the stimuli used but also on the manner in which participants' neural response to naturalistic stimuli are summarized.

While the current study was primarily concerned with examining trajectories of psychological states, as indexed by the trajectory of multi-voxel response patterns over time, we also tested whether similarities in multi-voxel response patterns themselves would be related to social network proximity. Our main analyses testing this relationship, in which response patterns to corresponding events were compared across participants (where events were defined based on major shifts in the narrative, in line with past related work, J. Chen et al., 2017; Zadbood et al., 2017), yielded null results. We also conducted an exploratory analysis in which inter-subject multi-voxel pattern similarities were summarized by TR rather than by event. This analysis implicated a single region in left early visual cortex where multi-voxel pattern similarity was significantly associated with social network proximity (Fig. S4). However, the results of this exploratory analysis should be interpreted with some caution, given that it was unplanned; these results are reported here in the spirit of completion and transparency.

Even in this exploratory analysis, we observed remarkable heterogeneity in the direction of the relationships between similarity in multi-voxel patterns and social network proximity across brain regions (Fig. S5). This is in marked contrast to the results of similar analyses relating social network proximity to multi-voxel pattern *trajectory* similarity across the whole experiment (Fig. 7) and across distal time points (Fig. 9), in which the overall trend was overwhelmingly positive in direction across most parcels. This difference in the overall pattern of results across analyses, combined with the fact that our main planned analyses of spatial pattern similarity yielded no significant results, suggests that whereas *trajectories* of multi-voxel patterns are exceptionally similar among friends in regions of the dorsal attention network, multi-voxel response patterns *themselves* are not consistently related to social network proximity.

These diverging results may be due at least in part to methodological differences between approaches. For example, between-subject comparisons of multi-voxel pattern trajectories effectively abstract away from the spatial layout of each subject's data, given that they compare individuals in terms of the relations between response patterns across time points, rather than in terms of the response patterns themselves (Kriegeskorte et al., 2008). This can be advantageous, given that aligning fMRI data to standard anatomical templates may not be sufficiently precise to align fine-scale response patterns across people, and also because there may not be considerable person-to-person correspondence in fine-scale spatial response patterns (Kriegeskorte and Bandettini, 2007). Therefore, between-subject comparisons of multi-voxel response patterns would likely be significantly influenced by between-subject differences in the functional response profiles of spatially corresponding voxels. Such differences could stem from limitations of anatomical alignment methods and/or from the fact that functional organization at this level of granularity is relatively idiosyncratic to individuals. This could make it comparatively difficult to pick up on psychologically meaningful sources of between-subject variability when analyzing multi-voxel response patterns directly. In contrast, multi-voxel pattern trajectories (and representational dissimilarity matrices in general, Kriegeskorte and Bandettini, 2007) are not bound to the spatial layout of each participant's data and thus are free from such limitations.

Future work focused on measuring individual differences with multi-voxel response patterns may benefit from the use of functional alignment methods, such as hyperalignment (Haxby et al., 2011) or the shared response model (P.-H. Chen et al., 2015). Such methods can help resolve misalignments in functional-anatomical correspondence between individuals, thereby circumventing some of the limitations of anatomical alignment methods when it comes to comparing fine-grained spatial patterns across subjects. That said, we note that previous work has found fine-grained response topographies evoked by naturalistic stimuli to be consistent across subjects (J. Chen et al., 2017) and meaningfully related to individual differences in how participants processed stimuli (Zadbood et al., 2017), even without the use of functional alignment methods. Thus, in the current study, the discrepancies between results based on multi-voxel pattern trajectories and multi-voxel patterns themselves may not only reflect methodological limitations. Rather, assessing inter-subject similarities in multi-voxel pattern trajectories (i.e., how states change over time) may capture similarities between friends that are simply not present in the multi-voxel response patterns (i.e., states) themselves. In other words, it is possible that friends share similarities in how their psychological states evolve over time, but the content of those psychological states at any particular point in time may be idiosyncratic to individuals and/or not systematically related to friendship.

In summary, we investigated the association between inter-subject similarity in the trajectory of multi-voxel response patterns to naturalistic audiovisual stimuli and individuals' proximity in a real-world social network. We found that people who share similar temporal trajectories of multi-voxel response patterns in the SPL were likely to be closer together in their shared social network. Thus, socially close individuals may experience a similar ebb and flow of endogenously-driven attentional states over time during natural stimulation. This may be driven by similarities related to friendship in people's expectations, interests, and dispositions, which in turn influence how attention is allocated to different aspects of external stimuli and to one's own internal representations and memories when viewing naturalistic stimuli.

More generally, the current results build on a growing body of research revealing systematic individual differences in neural responses during natural stimulation. Given the wealth of information that can be gleaned from analyzing distributed response patterns within brain regions, rather than only considering overall response magnitude (Norman et al., 2006; Haxby et al., 2014), researchers interested in individual differences in how people respond to the world around them may wish to use methods that are sensitive to such information. Yet, barriers to establishing fine-grained anatomical correspondences across subjects can make it difficult to compare multi-voxel patterns themselves across individuals. Fortunately, multi-voxel pattern trajectories may be more readily compared across individuals than multi-voxel response patterns. Thus, in future research, comparing individuals in this manner may prove to be a broadly useful way to examine individual differences in responses to naturalistic stimuli, given that this method takes into account both the topography of spatially distributed response patterns and how such response patterns fluctuate over time during exposure to dynamic, naturalistic stimuli.

Author contributions section

Ryan Hyon: Conceptualization, Methodology, Software, Formal analysis, Data curation, Writing - original draft, Writing - review & editing, Visualization. Adam M. Kleinbaum: Conceptualization, Methodology, Investigation, Resources, Data curation, Writing - review & editing, Project administration. Carolyn Parkinson: Conceptualization, Methodology, Investigation, Resources, Writing - original draft, Writing - review & editing, Project administration, Supervision.

Declaration of competing interest

The authors declare no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.neuroimage.2019.116492.

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