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## Sisterhood predicts similar neural processing of a film

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### ABSTRACT

Relationships between humans are essential for how we see the world. Using fMRI, we explored the neural basis of homophily, a sociological concept that describes the tendency to bond with similar others. Our comparison of brain activity between sisters, friends and acquaintances while they watched a movie, indicate that sisters' brain activity is more similar than that of friends and friends' activity is more similar than that of acquaintances. The increased similarity in brain activity measured as inter-subject correlation (ISC) was found both in higher-order brain areas including the default-mode network (DMN) and sensory areas. Increased ISC could not be explained by genetic relation between sisters neither by similarities in eye-movements, emotional experiences, and physiological activity. Our findings shed light on the neural basis of homophily by revealing that similarity in brain activity in the DMN and sensory areas is the stronger the closer is the relationship between the people.

### 1. Introduction

In their classical paper (Merton and Lazarsfeld, 1954) Merton and Lazarsfeld summarized “a tendency for friendships to form between those who are alike in some designated respect” by the single word “homophily”. Those sharing similarities of some sort get into contact more often than those who do not (McPherson et al., 2001). Moreover, such attraction to similar ones increases as a function of perceived similarity (Huston and Levinger, 1978). Recognizing similarity in others is often “reinforcing” (Clare and Byrne, 1974), modifying one's own attitudes and feelings towards them (Huston and Levinger, 1978). Further, similar others might be perceived as more attractive as the perceiver's projections concerning the likely consequences of future interaction with the stimulus person could play an important role: Both the alignment of attitude with one another (Reid et al., 2013) as well as the mutual trust (Singh et al., 2015) predict increased attraction. Individuals who share knowledge with one another are likely to interact

(Carley, 1991). Further, people who are at different “social distances” also have influences of different strengths on how we think, feel and act (Yamaguchi, 1990).

#### 1.1. Kinship premium

Kinship premium refers to preferring a family member over others (Machin and Dunbar, 2016; Madsen et al., 2007; Curry and Dunbar, 2011). Kin members are a special group. Family is a biosocial web of connections, based on shared ancestry and genotypes, leading to strong relationships that are stable between generations and gender, and survive long spatial and temporal distances (Pollet et al., 2013; Hamilton, 1964). Kin selection refers to the evolutionary strategy to favor the reproductive success of a relative (Hamilton, 1964). Family membership sets the grounds for a high similarity in fundamental social factors such as ethnicity, nationality, religion, language, social status and education (Bott et al., 1928; Loomis, 1946). Sistership is characterized by several

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similarities. Sisters do not only share 50 % of their genes, and have the same sex, but also have one of the longest-lasting relationship possible under normal conditions. Sisters have usually a quite similar age (e.g., compared to parents), and a similar social status within the family. Further, they share near-identical external factors, such as family size, nationality and ethnicity but also ties, tradition and practices as well as same heritage of religion, social status, values, and educational methods from their parents and mutual influence affecting especially in the first decade of their lives (Lee et al., 1990; McHale et al., 2012; Updegraff et al., 2005; Hamwey et al., 2019). They share experiences and memories from very early on. Thus, sisters share many external as well as in internal factors, this often translates into a very close emotional relationship.

### 1.2. Friendship

Friendships are crucial social relationships, which are not based on a genetic relation. We meet our friends frequently and they have an important emotional role in our lives (Dunbar, 2018). In addition to kin, friends form our innermost “support clique” of individuals that provide important emotional support. Similarly, as with siblings, friends often have a long-lasting relationship, but also share similarity in social class, age, gender or ethnicity (Verbrugge, 1977). Unlike with siblings, friendship has to be initiated actively, and meeting friends requires an opportunity (being in the same school, working in the same company, having the same hobby). A choice – intuitive or deliberate – is a more important factor in friendship than in kinship. In order to keep up a friendship, friends need to invest time in it and, e.g., chat about topics of common interest (Asher et al., 1998; Selman, 1980; Aboud and Mendelson, 1996; Bowker, 2004; Rubin et al., 1994). Friends tend to agree in values, opinions, interests, attitudes, beliefs and aspirations (Huston and Levinger, 1978; Richardson, 1940). They are often of similar intelligence, have the same occupation and abilities (Verbrugge, 1977; Podolny and Baron, 1997; Marsden and Gorman, 2001; Marsden, 1987; Louch, 2000). Such similarities are probably important in initiating a friendship, but friendship also makes friends more similar to each other over time.

### 1.3. Naturalistic stimulation

Interaction with others strongly shapes our behavior, and one factor influencing the strength of the shaping is the closeness of the relationship. An interesting question is to what extent the different types of relationships is reflected in the neural basis of mental processes. Can homophily also be characterized in neural terms? Recent advances in brain research methods have made it possible to start studying such complex phenomena. Human brain activity can be measured when subjects view an imitation of real-life like events, e.g. different types of films (Hasson et al., 2004, for a review, see (Jääskeläinen et al., 2021).

Even complete strangers share much of neural processing of naturalistic stimuli. During dynamic naturalistic stimulation, such as movie, subjects hemodynamic brain activity becomes synchronized, especially in the sensory processing areas but also in those involved in cognitive functions (Hasson et al., 2004; Jääskeläinen et al., 2008; Lahnakoski et al., 2014; Malinen et al., 2007) and across modalities (Saalasti et al., 2019; Wilson et al., 2008; Regev et al., 2013). Further, ISC may not only reflect mutual neuronal responses, but could provide the basis of inducing a specific common mind set, e.g. built by contextual information or perspective-taking as well as predicting the actions of others. Taking the same perspective when watching a movie has been shown to increase the synchrony of subjects brain activity patterns when being in the same perspective e.g. when comparing the perspective of a crime inspector (social) vs. an interior decorator (non-social) (Lahnakoski et al., 2014) or two social perspectives in a moral dilemma (Bacha-Trams et al., 2020) A further fMRI study using a movie as stimulus on the cognitive style of subjects (Bacha-Trams et al., 2018) revealed increased

brain pattern synchrony (measured as ISC) between subjects that self-reported to follow either a holistic or analytical thinking style that have been characterized in Eastern vs. Western cultures (Choi et al., 2007). These thinking styles were shown to be reflected in the brain activity patterns of the subjects with holistic thinkers showed significant ISC in more extensive cortical areas than analytical thinkers, suggesting that they perceived the movie in a more similar fashion.

### 1.4. Homophily

Recently, Parkinson et al. (Parkinson et al., 2018) showed that when friends vs acquaintances viewed a set of film clips, brain activity of friends was more similar than that of acquaintances. Strength of similarity was dependent on the distance of the subjects in the social network, decreasing when the distance increased. In more recent studies, Hyon et al., (Hyon et al., 2020) as well as McNabb et al., (McNabb et al., 2020) investigated interpersonal similarity in functional connectivity at rest. Interestingly, whereas (Hyon et al., 2020) found a positive relation between functional connectomes and social network proximity, particularly in the default mode network, the study of McNabb (McNabb et al., 2020) did not observe significant relationships between social distance, community homogeneity and similarity of global-level resting-state connectivity in data from 68 school-aged girls with social network information from all pupils in their year groups (total 5066 social dyads). Thus, while neural homophily has been shown between friends viewing naturalistic stimuli, the findings for functional connectivity at rest are mixed and thus the influence of resting-state connectivity on a person's social environment may be less prominent.

### 1.5. The present study

In the present study, brain activity was measured with fMRI when subjects viewed a feature movie and was analyzed with voxel-wise inter-subject correlation (ISC) of hemodynamic activity in order to estimate the similarity of neural processing of subjects (Hasson et al., 2004; Malinen et al., 2007; Pajula et al., 2012; Ylipaavalniemi et al., 2009; Bartels and Zeki, 2004). Specifically, we asked if the neural processing of sisters is more similar than that of friends, and further if the neural processing of sisters and friends is then more similar than that of acquaintances. In addition, we analyzed the anatomical similarity, eye movements as well as heart rate and breath frequency of the subjects. After the scanning, the subjects viewed the film again and indicated their experienced valence and arousal (Nummenmaa et al., 2012). We hypothesized that all participant groups have similar neural activity in their auditory and visual processing areas, as well as prefrontal areas and default-mode network, as shown in previous studies using similar stimulus material (Jääskeläinen et al., 2008; Hasson et al., 2010). In addition, we hypothesized that we find stronger similarity in the brain activity between sisters than between friends, and between friends than between acquaintances. We controlled for the possible similarity of sisters' gross brain anatomy in explaining the results.

## 2. Materials and methods

### 2.1. Subjects

From the 33 healthy female subjects (19–39 years, mean age of 26 years, one left-handed, laterality index of right-handed 84.5 %), three subjects were excluded due to discomfort in the scanner, so that the final analysis included 30 subjects. None of the subjects reported any history of neurological or psychiatric disorders and reported either normal or corrected to normal vision by contact lenses. The participants consisted of 10 triplets of subjects with each triplet containing a pair of sisters and a female friend of one of the sisters who was at the same time an acquaintance of the other sister. All the experimental protocols were carried out in accordance with the guidelines of the declaration of Helsinki

and further approved by the research ethics committee of the Aalto University (Lausunto 9 2013 Sosiaalisen kognition aiomekanismit, 8.10.2013). Written informed consent was obtained from each subject prior to participation.

## 2.2. Stimuli and procedure

The results shown in this article were acquired as a part of a larger dataset. All subjects watched an identical video stimulus, which was an edited version of 23 minutes and 44 s based on the movie *My Sister's Keeper*™ (dir. Nick Cassavetes, 2009, Curmudgeon Films) during functional magnetic resonance imaging (fMRI). The movie depicts the moral dilemma of refusal of an organ donation between two sisters: The younger Anna is asked to donate one of her kidneys to her sister Kate, who is fatally ill from cancer, but refuses to agree in the donation. As consequence Kate dies. The reason for Anna refusing to donate the kidney was not revealed to the subjects until after the experiment. The movie was shown to the subjects in the scanner in different conditions (see Bacha-Trams et al., 2018 for details). The results of the other aspects that resulted from this dataset, e.g. the differences between the conditions of genetic vs adoptive sisters, and the two perspectives as well as the a comparison of the perception of the movie in participants with either holistic or analytical thinking style, are reported in separate publications (Bacha-Trams et al., 2020; Bacha-Trams et al., 2018; Bacha-Trams et al., 2017). In addition, the subjects took part in a moral-dilemma decision task during fMRI in order to localize brain regions that are related to moral decision making (see Bacha-Trams et al., 2017 for details).

## 2.3. fMRI acquisition and analyses

### 2.3.1. fMRI acquisition

fMRI data were acquired when the subjects watched the edited movie. Each participant watched the movie for four times, twice in two sessions recorded on two different days of scanning. The movies were shown under four different conditions (hence four times of watching): the participants were asked to watch the movie from the perspective of one (Anna) or the other sister (Kate). Further, the participants were told in the different sessions of scanning that the two movie protagonists Anna and Kate would be genetic sisters or that the younger one would be adopted at birth. For the analysis between relationship groups all four sessions were analyzed in combination. Before starting to scan all subjects were informed about the scanning procedures and asked to avoid bodily movements during the scans. The stimuli were shown to the subject in the scanner using the Presentation software and over a semitransparent screen using a data projector as well as an audio system (see Bacha-Trams et al., 2017 for details). The fMRI data were recorded at the Advanced Magnetic Imaging center, Aalto University, with a 3T Siemens MAGNETOM Skyra (Siemens Healthcare, Erlangen, Germany) using a standard 20-channel receiving head-neck coil (see Bacha-Trams et al., 2017 for details). For each movie viewing 712 whole-brain EPI volumes were acquired while for the moral dilemma decision task the number of whole-brain EPI volumes varied according to the individual time taking for the decision to be made by each subject (median 267 whole-brain EPI volumes). Accompanying the fMRI measurements, heart and breathing rate were monitored with the Biopac system (Biopac Systems Inc., Isla Vista, California, USA) and the resulting values were analyzed with Drifter software package 55 (<http://becs.aalto.fi/en/research/bayes/drifter/>).

### 2.3.2. fMRI preprocessing

Standard fMRI preprocessing steps were performed using the FSL software ([www.fmrib.ox.ac.uk](http://www.fmrib.ox.ac.uk)) and custom MATLAB code (available at <https://version.aalto.fi/gitlab/BML/bramila/>) EPI images were corrected for head motion using MCFLIRT and co-registered to the Montreal Neurological Institute's 152 2 mm template in a two-step registration

procedure using FLIRT. First, the EPI is registered to the subject's anatomical image after brain extraction (9 degrees of freedom) and second the registration from anatomical to standard template (12 degrees of freedom) applies. To remove scanner drift, we applied high-pass temporal filter at a cut-off frequency of 0.01 Hz and spatial smoothing with a Gaussian kernel of 6 mm full width at half maximum. In order to remove artifacts from the BOLD time series 24 motion-related regressors were applied to control for signal from deep white matter, ventricles and cerebral spinal fluid locations (see Power et al., 2014 for details). For quality control, framewise displacement was computed to quantify instantaneous head motion. Out of all the 120 runs (30 subjects, 4 sessions each), 97.5 % of the runs (117 runs) had 90 % of time points (640 volumes) with framewise displacement under the 0.5 mm threshold as suggested in (Power et al., 2012). Of the remaining three runs, only one session had a considerable amount of head motion (the number of time points under 0.5 mm were 489 (68.7 %) as well as 639 (89.7 %), 633 (88.9 %) for the two others). This session was removed from the dataset. While head motion might be a concern in connectivity studies, in across-brain time series correlation, head motion had been found to reduce the signal-to noise-ratio. To anyway be sure that head motion similarity did not explain any group difference, the same permutation test as for the ISC was computed for average framewise displacement by estimating the similarity of two subjects as the distance between their average framewise displacement value. The analysis showed that in average head motion was not different between the two viewing conditions ( $t = 0.255$ ;  $P = 0.398$  obtained with 5000 permutations).

### 2.3.3. Inter-subject correlation (ISC) analysis of brain activity during movie watching

In order to examine how similar the brain activity was across subjects in the different experimental conditions, inter-subject correlation (ISC) was conducted using the isc-toolbox (<https://www.nitrc.org/projects/isc-toolbox/>) (Kauppi et al., 2010). With the toolbox software a similarity matrix is computed, for each voxel between subject pairs and within the same subject in all conditions, with the conditions being (i) shared assumption that the movie's sisters are genetically related, (ii) shared assumption that the younger sister was adopted, (iii) shared perspective of the to-be-organ-donor, and (iv) shared perspective of the to-be-organ-recipient. The resulting matrix has a total size of  $120 \times 120$  (4 conditions  $\times$  30 subjects). Each value of the correlation matrix is a result of the correlation between the BOLD time series of the pair of subjects considered for the selected voxel. We created a model matrix ( $120 \times 120$ ) defining the pairs of relationship groups (sisters, friends and acquaintances) with 10 pairs for each group. This matrix was then compared against the ISC matrices of the brain activity during the movie watching: For each voxel, the overall ISC differences between participants of the different relationship groups were examined by contrasting the 10 pairs of each group. The differences of ISC between the relationship groups are then computed by using the Fisher Z transform to transform the correlation values into z-scores and then computing t-values and corresponding P-values using a permutation-based approach (Glerean et al., 2016). Further, to correct for the multiple comparison, a Benjamini–Hochberg false discovery rate (BH-FDR) correction at a  $q < 0.05$ , corresponding to a t-value threshold of 2.133, was conducted. For visualization purposes, a cluster correction was performed by removing any significant cluster smaller than  $4 \times 4 \times 4$  voxels and summary tables were generated with an increased t-value threshold of 3.

Unthresholded statistical parametric maps can be found in neurovault: <https://neurovault.org/collections/ULZAPFRX/>. To further explore the effect of the relationship contribution in the values of intersubject correlation while controlling also for the task that the subjects were doing in the scanner, we also performed a multiple linear regression model analysis with the intersubject correlation values as the dependent variable modelled with the following dependent variables: group membership of the pair (sisters, friends, acquaintances),



protagonist perspective task (Anna's perspective, Kate's perspective), adopted versus non-adopted, value of eye tracking inter subject correlation for the pair. For computational reasons this analysis was conducted on regions of interests as described in section 2.1.4. Results are reported in a supplementary information file. The code for this analysis is available at <https://github.com/eglearean/sisterhoodfmri>.

#### 2.3.4. Inter-subject functional correlation (ISFC) analysis of brain activity during movie watching

In addition to the ISC analysis, to explore the connectivity between brain regions involved in the task, we computed the inter-subject functional correlation connectivity matrix.

For each subject we computed region of interest (ROI) BOLD time series for 264 nodes based on the functional parcellation by Power et al. (2011). BOLD time course were extracted for each node within a 1-cm diameter sphere centered at each node's coordinates (list of coordinates and module assignments available at [https://web.archive.org/web/20160127134525/http://www.nil.wustl.edu/labs/petersen/Resources\\_files/Consensus264.xls](https://web.archive.org/web/20160127134525/http://www.nil.wustl.edu/labs/petersen/Resources_files/Consensus264.xls)).

To compute ISFC for each individual, the Pearson correlation coefficient is calculated between that participant and the average time series for all other N-1 participants. This approach resulted in individual level connectivity matrices of  $264 \times 264$  nodes. Statistical significance for each link was assessed by first estimating the link null distribution using permutations by circularly time-shifting the data. Surrogate null distributions were computed over 4.8 million permuted values. Then, for each connectivity link an uncorrected p-value was calculated based on the kernel smoothed estimated cumulative distribution function. Finally, Benjamini-Hochberg False Discovery Rate correction was applied across all links p-values of the network. The code for this analysis is available at <https://github.com/eglearean/sisterhoodfmri>. Results were summarized using the, 10 subnetworks of functional systems of interest as proposed by Power et al. (2011), which comprised the following networks: motor and somatosensory (35 nodes), cingulo-opercular (14 nodes), auditory (13 nodes), default mode (58 nodes), visual (31 nodes), fronto-parietal (25 nodes), salience (18 nodes), subcortical (13 nodes), ventral attention (9 nodes), and dorsal attention (11 nodes) networks.

#### 2.3.5. General linear model analysis of the fMRI data acquired during a moral dilemma localizer task

A moral dilemma decision task was performed by all subjects to localize regions involved in moral processing and analyzed with a general linear model approach using the SPM12 software ([www.fil.ion.ucl.ac.uk/spm](http://www.fil.ion.ucl.ac.uk/spm)). A temporal model of the occurrence of decision moments was created with the decision regressor including time points from the revelation of the identity of involved individuals to the moment of decision indicated by button press. Brain activity during these time points was compared to the activity in all other time points of the task, e.g., time points telling the background story of the moral dilemma in the presentation. To account for hemodynamic lag, the regressors were convolved with canonical hemodynamic response function. In addition, the preprocessed input data (see above) were high-pass filtered (cutoff 128 s) to remove low-frequency signal drifts. In the first level analysis main effects of the regressors were generated from individual contrast images and then in the second-level analyses were performed in MATLAB: one-sample t-test over subjects showed significant activations in decision vs. no decision moments. Statistical threshold was set at  $p < 0.05$  (cluster-corrected using the threshold free cluster enhancement approach implemented by FSL randomize with 5000 permutations).

### 2.4. Physiological data recording and analyses

#### 2.4.1. Recording and analysis of eye-movements

Eye movements were recorded from all subjects during fMRI scanning using an EyeLink 1000 eye tracker (see Bacha-Trams et al., 2018 for details). For the analysis, subject-wise gaze fixation distributions were

compared across relationship groups (see Bacha-Trams et al., 2018 for details).

The statistical significance of the group differences was analyzed by contrasting the pairs representing sister, friend and acquaintance relationships with the non-parametric Kruskal-Wallis test.

#### 2.4.2. Heart rate and breathing rate analysis

Accompanying the fMRI measurements, heart and breathing rate were recorded and analyzed for each subject in order to exclude these factors in implications on the fMRI measures as well as to examine if there were differences between the movie watching conditions and finally to investigate if any correlation between the heart and breathing rate and other measures of the study could be found. Differences between the relationship groups were computed in the same way as in the ISC analysis: correlation values were transformed into z-scores with Fisher Z's transform, and then a non-parametric Kruskal-Wallis ANOVA test was used to compute p-values between the groups.

#### 2.4.3. Anatomical measures

To quantify morphological similarities (based on magnetic resonance images) between sisters, friends and acquaintances we analyzed the brain data using FreeSurfer and ShapeDNA, a software package for analyzing similarities in the shape of the brain. The shape representations (eigenvalues of Laplace-Beltrami operator) were computed for white matter surfaces of the brains of sisters, friends and acquaintances. The Euclidean distances between eigenvalues can be regarded as a similarity measure between subjects. The closer the eigenvalues are between subjects, the more similar their brains anatomically are. T-tests were performed to compare the similarity of patterns of sisters, friends and acquaintances.

### 2.5. Behavioral measurements and self-reports

#### 2.5.1. Self-reports

In addition to brain imaging and physiological data acquisition, the subjects provided several self-reports. After the first fMRI session, all subjects were asked to answer five short freeform questions about their perception of the movie, specifically about how easy it was to take one or the other perspective, and whether they would have donated their kidney if in place of the movie protagonist.

After the second fMRI session, a debriefing took place for the subjects as they were shown the ending of the original movie, where it is revealed that the sick sister had wished for the healthy sister to refuse donating her kidney. After watching the ending, the subjects were asked to state if the seeing the real ending changed their opinion on the roles of the two movie protagonists. Further the subject reported their social network including their emotional closeness to their sister and best friend in a questionnaire (Roberts and Dunbar, 2011).

As an additional self-report measure, the subjects' disposition for catching emotions from others was assessed with two emotional empathy questionnaires: Hatfield's Emotional Contagion Scale and the BIS/BAS scale (Hatfield et al., 1994; Carver and White, 1994). Hatfield's Emotional Contagion Scale is composed by 18 questions to be answered using a 4 point Linkert scale, resulting in a score between 18 and 72. The BIS/BAS scale however comprises four 5 point Linkert subscales to measure (i) the behavioral inhibition system (BIS), as well as the behavioral activation system with the aspects (ii) BAS Drive (motivation to follow one's goals), (iii) BAS reward responsiveness (sensitivity to pleasant reinforcers in the environment) and (iv) BAS fun seeking (motivation to find novel rewards spontaneously). In addition, after viewing the movie for the last time, each participant was asked to answer a 24-item questionnaire (Choi et al., 2007) to assess their thinking style as either holistic or analytical. This aspect of the study was analyzed and published separately (Bacha-Trams et al., 2018).

### 2.5.2. Valence and arousal measurements

To test whether self-reported emotions experienced during movie viewing were different between relationship group dynamic valence and arousal measurements were compared between sisters, friends and acquaintances. After the fMRI experiment, all subjects watched the movie again and emotional valence (positive-negative scale) and arousal which were acquired on separate runs (full procedures have been described in an earlier publication: (Nummenmaa et al., 2012). During movie watching the subjects rated the their current state of valence or arousal by using a small cursor on the right side of the screen up and down in the web tool <https://version.aalto.fi/gitlab/egleean/dynamicannotations> (Nummenmaa et al., 2014). The self-ratings were collected at 5 Hz sampling rate. To analyze differences between the relationship groups inter-subject similarity matrices using valence and arousal rating time-series were computed. After that the values of the correlation matrices were compared by computing the p-values using the Kruskal-Wallis one-way ANOVA tests.

## 3. Results

### 3.1. Intersubject correlation

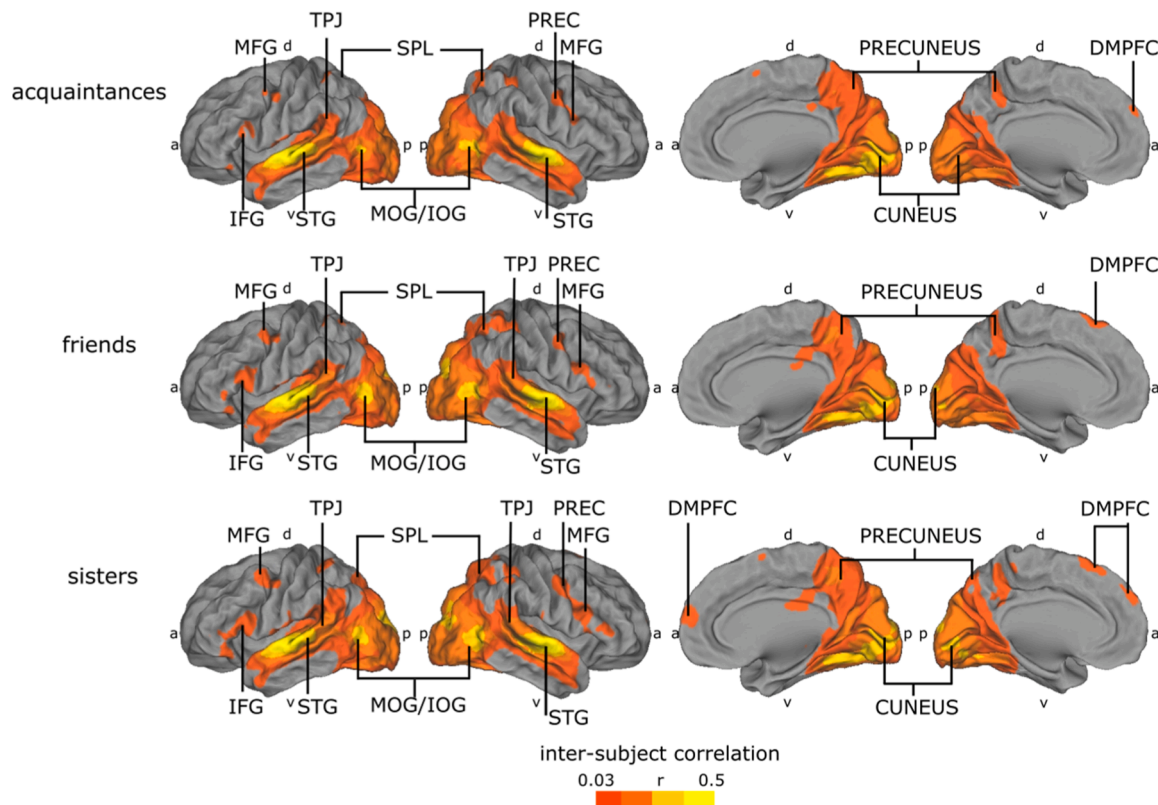
Fig. 1 depicts ISC calculated separately for acquaintances, friends and sisters. ISC is strongest in bilateral temporal auditory (STG, MTG)

and visual (MOG/IOG) cortical areas, as well as in medial visual cortical areas (Cuneus), and in Precuneus. Significant ISC is also found in the bilateral temporal-parietal junction (TPJ) and the superior parietal lobule (SPL). In the lateral frontal cortex, ISC is significant in the medial frontal gyrus (MFG), inferior frontal gyrus (IFG) and, as well as in superior frontal gyrus (SFG), and medially in ventro-medial prefrontal cortex (VMPFC) and dorso-medial prefrontal cortex (DMPFC).

However, there are some interesting differences in relatedness groups (see Fig. 2). For example, ISC in bilateral frontal cortical areas and DMPFC is especially high in sisters, and such activity is much smaller in acquaintances.

Fig. 2 shows significant pairwise contrasts in the ISC strengths of the relatedness groups. As depicted at top, ISC was stronger in sisters vs. acquaintances in several brain areas of the frontal (MFG, IFG, SFG, Frontal pole), parietal (precentral gyrus, (PREC), TPJ, SPL) and occipital cortex (MOG/IOG). In addition, ISC was stronger in bilateral Precuneus and Cuneus.

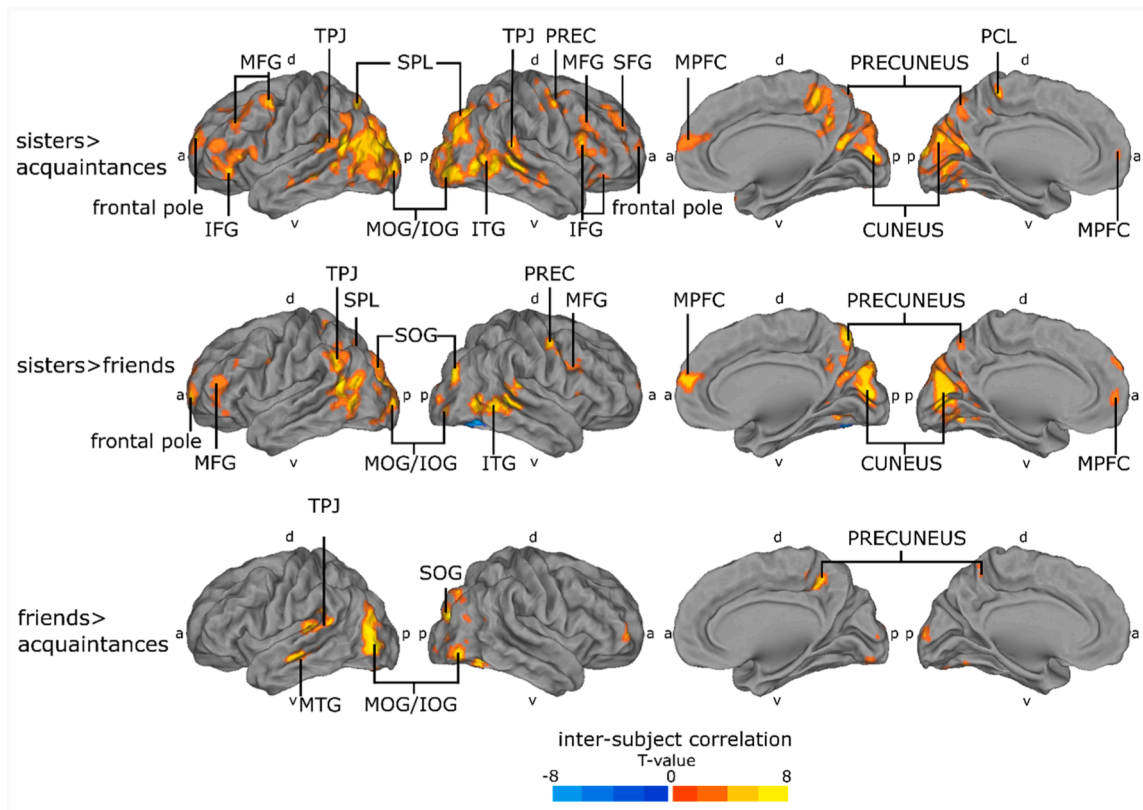
ISC was also stronger in sisters vs. friends, but in a more limited set of areas than in the contrast described above. Significant differences were found in the left frontal pole and bilateral MFG, left TPJ and SPL, right inferior temporal gyrus (ITG), bilateral superior occipital gyrus (SOG), right PREC, midline medial pre-frontal cortex (MPFC), Precuneus and Cuneus. There was also a difference between friends vs. acquaintances. Friends showed stronger ISC in left TPJ and medial temporal gyrus,



**Fig. 1. Inter-subject correlation (ISC) of specific kinship groups.**

ISC between participant pairs of acquaintances, friends and sisters irrespective of the condition under which the participant watched the movie. The whole-brain analysis revealed high correlation between sisters in wide parts of the parietal, temporal and occipital cortices as well as in parts of the frontal cortex, both laterally and medially. The correlated brain areas were not restricted to areas of basic perception but also comprised higher order associative areas. Sisters show ISC in the whole occipital cortex, as well as large parts of the temporal (STG, MTG, TPJ) and parietal (SPL; cuneus, precuneus) cortices. In the frontal cortex ISC is particularly found in the IFG, MFG and parts of the SFG. Friends still show high correlations in various areas of the occipital and temporal lobe, but fewer ISC in the parietal lobe and frontal cortex. Correlation is seen in the inferior frontal gyrus, superior frontal region (MFG, DMPFC), temporo-parietal junction (TPJ) as well as medial dorsal frontal cortex. For acquaintances ISC still decreases with a main focus of correlated areas in basic auditory and visual perception as well as in the inferior frontal gyrus, middle frontal gyrus, temporo-parietal junction, superior parietal lobe as well as medial dorsal frontal cortex (DMPFC).

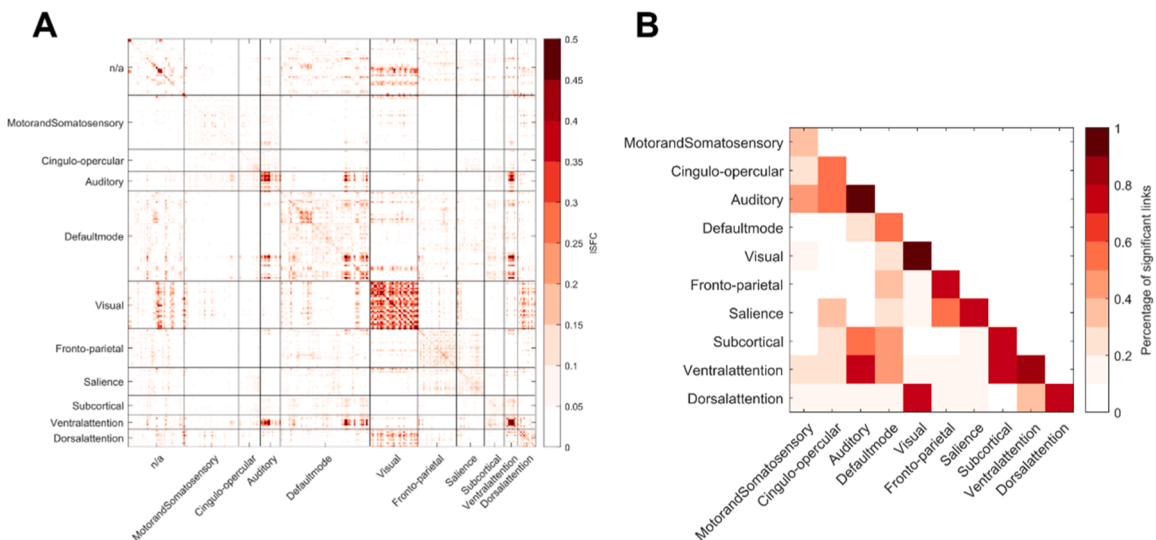
Abbreviations: DMPFC = dorsomedial prefrontal cortex, IFG = inferior frontal gyrus, IOG = inferior occipital gyrus, MFG = middle frontal gyrus, MOG = medial occipital gyrus, PREC = precentral gyrus, SFG = superior frontal gyrus SPL = superior parietal lobule, STG = superior temporal gyrus, TPJ = temporo-parietal junction, VMPFC = ventromedial prefrontal cortex.



**Fig. 2.** Contrasts of Inter-subject correlation (ISC) between different relationship groups.

ISC contrasts between participant pairs of acquaintances, friends and sisters, i.e. the brain areas which are specifically higher correlated in each group. High ISC becomes visible for sisters, particularly in lateral (middle and inferior occipital gyrus) and medial (Cuneus) occipital cortex, the lateral (SPL) and medial (Precuneus) parietal cortex, posterior parts of the inferior temporal gyrus as well as in the lateral (MFG, IFG and frontal pole) and medial (MPFC, VMPFC) frontal cortex. Comparing sisters vs. friends, higher correlated areas were found for sisters in the MOG/IOG, SPL, TPJ, ITG, MFG, frontal pole, precuneus, cuneus, MPFC, and VMPFC. The DMPFC shows a unique contrast for this comparison. Friends and acquaintances differ mainly in their correlation in MOG/IOG, TPJ, precuneus and cuneus. Areas in the MFG and MTG show a specific contrast when comparing friends to acquaintances.

Abbreviations: DMPFC = dorsomedial prefrontal cortex, IFG = inferior frontal gyrus, IOG = inferior occipital gyrus, ITG = inferior temporal gyrus, MFG = middle frontal gyrus, MPFC = medial prefrontal cortex, MOG/ = medial occipital gyrus, MTG = middle temporal gyrus, PREC = precentral gyrus, SFG = superior frontal gyrus, SOG = superior occipital gyrus, SPL = superior parietal lobule, STG = superior temporal gyrus, TPJ = temporo-parietal junction.



**Fig. 3.** A) the full adjacency matrix of significant links is shown. The 264 nodes are rearranged to follow the subnetwork labeling as specified in Power et al. 2011. Only FDR corrected values are visualized. B) This figure offers a summary of the full adjacency matrix by looking at the percentage of significant links within or between subnetworks, i.e. the fraction of links that are significant, divided the total number of all possible links between the network pair considered.



MTG, right SOG, bilateral medial/inferior occipital gyrus (MOG/IOG) and midline Precuneus. The overall picture from these two analyses is that similarity of brain activity varies in the order: Sisters > Friends > Acquaintances.

### 3.2. Intersubject functional connectivity analysis

The stimulus-dependent connectivity (ISFC) between brain areas across the whole movie is reported in Fig. 3 for each link (Fig. 3A) and is also summarized as percentage of significant links (Fig. 3B) in each subnetwork and between subnetwork pairs. The ISFC analysis clearly shows an important involvement of within network connectivity in primary sensory areas as well as the visual and dorsal attention subnetworks. When looking at connections between subnetworks, while auditory-ventral-attention-subcortical had a large percentage of significant connectivity links, the default mode network was the network significantly connected with almost all other networks.

### 3.3. Structural brain anatomy in sisters and friends

We examined the possibility that the strong ISC in sisters is based on similarity of their brain anatomies. Comparing the gross brain anatomy (gyri and sulci), the mid-sagittal visualizations show no clear pattern of similarity between sisters or friends. Further, to quantify the morphological similarities (based on magnetic resonance images) between sisters, friends and acquaintances we analyzed the brain data using FreeSurfer and ShapeDNA, a software package for analyzing similarities in the shape of the brain. In the analysis we could not find any pattern of sisters having shorter distances between the eigenvalues compared to other pairs (Fig. 4). The results of a *t*-test show that only compared to strangers, the sister pairs have slightly more similar brain shapes ( $t = 1.866$ ;  $p = 0.043$ , uncorrected). Compared to friends, there is no evidence of sisters being more similar in their brain morphology.

### 3.4. Physiological, behavioral and eye tracking analysis

To control that differences between the relatedness of groups cannot be explained with differences in the viewing behavior, physiological measurements or behavioral ratings as for valence and arousal, these data were compared between the relationship groups (non-parametric Kruskal-Wallis ANOVA test). No differences in mean eISC of the eye gaze was observed between groups ( $X^2(2, N = 135) = 4.17, p = 0.1244$ ). Further no significant differences were found in the valence and arousal measurements (Valence:  $X^2(2, N = 27) = 0.6, p = 0.7414$ ; Arousal:  $X^2(2, N = 29) = 2.33, p = 0.3119$ ), and heart and breathing rate (Heart rate:  $X^2(2, N = 472) = 0.13, p = 0.9388$ , Breathing rate:  $X^2(2, N = 472) = 0.86, p = 0.6490$ ), between the groups of sisters, friends and acquaintances. Fig. 5 shows the data for valence and arousal rating, physiological heart and breathing rate, as well as eye tracking between the relationship groups.

The questionnaires on emotional contagion showed very similar results with low variance between the subjects: the average of Hatfield's Emotional Contagion Scale lays at 50.73 points (range 18–72 points, s.d. = 5.06) and the subjects scored on the BIS scale with 21.72 (s.d. = 3.61 range 7–35) as well as on the BAS drive with 13.97 (s.d. = 2.73, range 5–25), on the BAS fun seeking with 20.86 (s.d. = 2.50, range 5–25) and on the reward responsiveness with 15.10 (s.d. = 2.93, range 4–20).

## 4. Discussion

### 4.1. Social relationships

Humans differ in how similar they are to others in their brain patterns when processing the same events. In this study, we investigated how the neurocognitive processing of individuals with different social

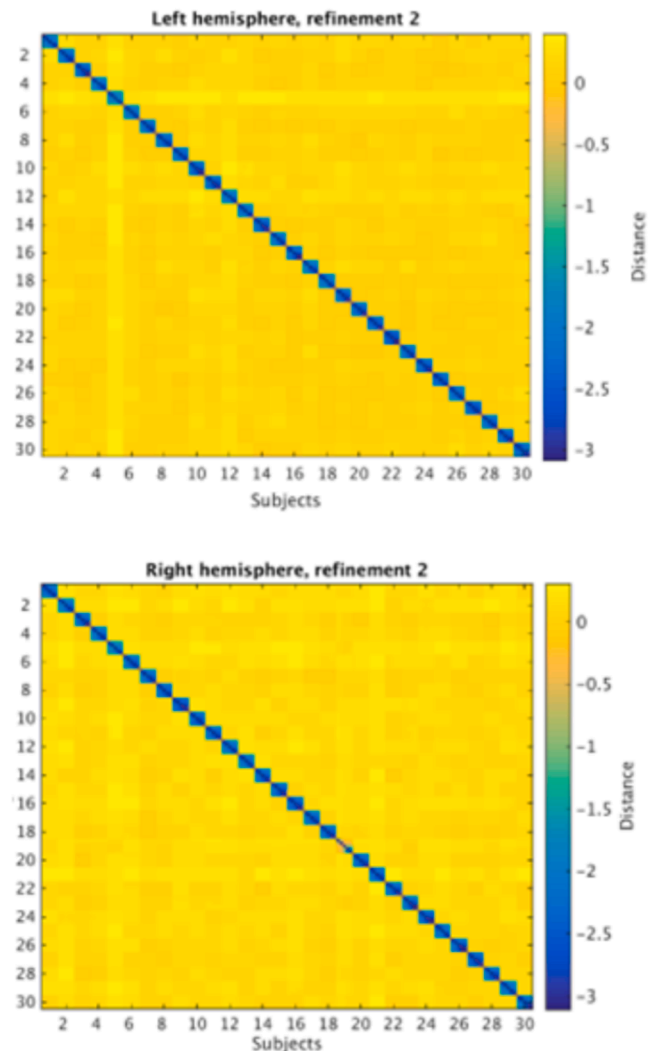


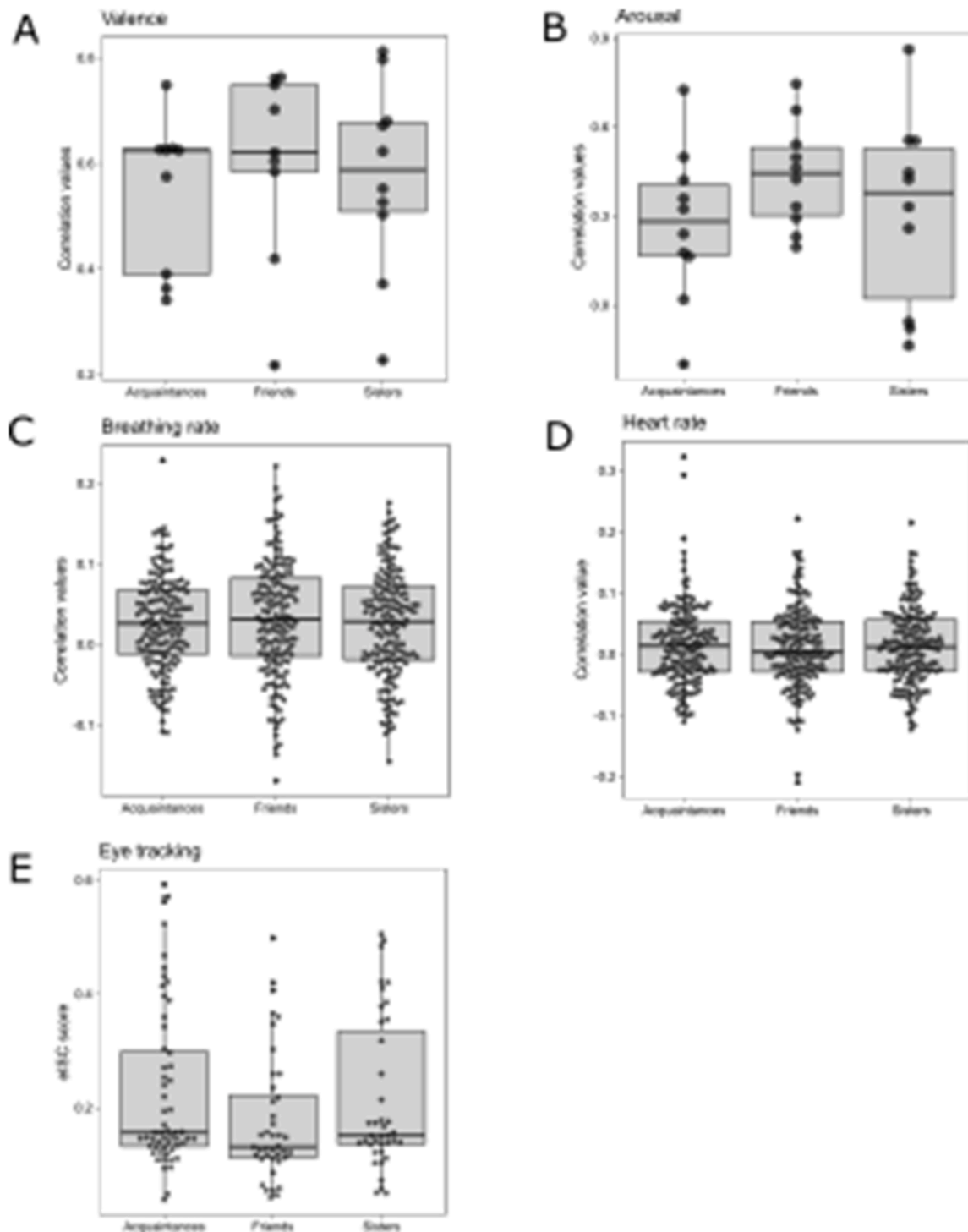
Fig. 4. No structural similarity for sisters.

No visible similarity of sisters (located next to each other in matrices) could be observed as distances are not shorter between the eigenvalues of sisters compared to other pairs.

relationships compare under naturalistic conditions with following the hypothesis that similarities in brain activity patterns may be correlated to the closeness of their relationship. More specifically we examined if pairs of sisters, friends or acquaintances would show more similar brain activity patterns when watching a movie showing a moral dilemma depicting the refusal of an organ donation between two sisters during fMRI.

Sisters, often having a close emotional relationship that is potentially the longest lasting relationship of their lives, consequently, resemble in many external and internal factors. However, also friends are sharing emotionally founded long relationships, and further show similarity in aspects as social class, age, gender or ethnicity. Furthermore, possibly elicited by the need to belong, friends tend to resonate with each other in factors as values, opinions, interests, attitudes, and beliefs. Acquaintances, the third group of examined subjects, show similarities via inclusion in the same socioeconomic, ethnic, religious and age groups but without forming a noteworthy emotional bond or a frequent contact with each other. Thus, when aiming at going beyond comparing strangers to closer relationships (as siblings and friends), considering acquaintances, we are able to hold some basic factors stable and study an intermediate level of relations which is neither too proximal to friendship nor, too far from it.





**Fig. 5.** No significant differences in valence and arousal rating, physiological heart and breathing rate, as well as eye tracking between the relationship groups.

The analyses using non-parametric Kruskal-Wallis ANOVA tests revealed no significant differences in between the groups of sisters, friends or acquaintances.

In this study a movie depicting a moral dilemma regarding organ donation was used as a naturalistic stimulus. Viewing such a situation of a moral dilemma is emotionally and socially complex and engages the attention of the viewers. The potentially life-threatening situation presented in the form of moral dilemma increases the immersion of the study participants into the situation and guide them to relate to the severity of either decision's consequences. Thus, it may strengthen the similarity of perception compared to a less dramatic situation, as threat

is a factor to narrow down the patterns of brain activity (Molenberghs and Louis, 2018; Chang et al., 2016; Henry et al., 2009; Chekroud et al., 2014; Domínguez D et al., 2018).

#### 4.2. Brain activity associated to homophily

To investigate if participants with differing, but close, relationships show parallel differences in the neural processing of the naturalistic

moral dilemma, ISC was determined for each relationship group (Fig. 1 and 2). The results show that the ISC underlying the movie perception differs indeed between the group of sisters, friends, and acquaintances: It is clearly shown that highest correlations exist between sisters, followed by the correlations between friends. Less ISC is found for acquaintances. In the following, we will describe the involved neuronal networks and discuss their potential functions and implications in social processing. Even though suggestions of brain functions are made, we are well aware of the caveats associated with reverse inference (Poldrack, 2011), although see (Hutzel, 2014) and wish to caution the reader to keep them in mind.

When comparing the brain activity patterns between sisters, friends and acquaintances during the movie viewing, we found many areas that show a contrast in the comparison of sisters vs. acquaintances are also higher correlated in sisters than in friends. However, differences between sisters and friends are slighter than between sisters and acquaintances.

Specifically, the TPJ, the precuneus the PREC, inferior frontal and middle frontal gyri and insula (IFG and MFG) as well as the left frontal pole, and the right ITG and the right MPFC were highly correlated. Many of these areas are neuronal hubs in the DMN and have been found to be highly correlated in this study particularly between the pairs of sisters.

As a first brain region that is often considered as a part of the DMN, the precuneus has shown higher ISC between sisters than between friends and acquaintances. The left precuneus has been shown to be an important hub for mentalizing and theory of mind processes (Atique et al., 2011). Moreover, it has been shown that the precuneus is involved in moral reasoning. Pujol et al., 2008, have found the precuneus to be active when making a moral dilemmatic decision, as well as when watching the outcome of that decision (Pujol et al., 2008). Parkinson et al., 2011 showed an involvement of the precuneus when subjects were judging moral dilemmas that focus on dishonest behaviour (Parkinson et al., 2011). As its left counterpart, the right Precuneus has been associated with social and emotional processing (Rudie et al., 2011; Kross et al., 2011). Thus the higher ISC of sisters in the precuneus could reflect their more uniform perception and evaluation of the moral dilemma of the refused organ donation.

The TPJ is a further brain area of the DMN, that is higher correlated in sisters than in friends and acquaintances in both hemispheres. The TPJ has been shown to have an important role in mentalizing, theory of mind and social processing: The TPJ is e.g. specifically activated in mentalizing about the self and others (Lombardo et al., 2010; Kestemont et al., 2013; Kestemont et al., 2015), emotion mentalizing and intention mentalizing (Atique et al., 2011), processing of social emotion (Burnett and Blakemore, 2009), belief reasoning (Van der Meer et al., 2011) and perspective taking (Bacha-Trams et al., 2020; Van Elk et al., 2017). Thus, one might suggest that the group of sisters showed more similar activation in brain regions associated with social and moral reasoning than the other groups while watching the movie.

The MPFC is a third region of the DMN, which was found to be highly correlated in sisters, has been associated to play a crucial role in self-knowledge and self-reference (Ochsner et al., 2005) and mentalizing about the self and others (Lombardo et al., 2010; Van Overwalle, 2009; Amodio and Frith, 2006; Singer et al., 2004). Furthermore Singer et al., (Singer et al., 2004) have shown that this area is a part of a system associated with social cognition, that can recognize the learned moral status of a face (showing increased activity for a face of a co-operator in a moral action). It can be assumed that the evaluation of the moral dilemmas, involves a deep exploration of individuals' motives and how they relate to one's own values. These processes could be more similar in sisters than in other relationship groups. Further, the social relevance of emotional stimuli could resemble more closely between sisters than between other study participants: When comparing socially emotional images with biological images the MPFC showed greater activity for the former (Sakaki et al., 2012), which may suggest that the processing of social stimuli involves elaborative processing requiring frontal lobe

activity, which could be more similar between sisters. Another possible explanation could be the ambiguity of the moral decision: both decision alternatives, to donate the kidney or not to do so, could be built on sound arguments, thus the decision is far from being clearly right or wrong and rather ambiguous. Brain activity in the medial prefrontal cortex has been shown to be modulated by ambiguity in social contexts (Jenkins et al., 2014)

#### 4.3. The default mode network

The DMN has been shown to be relevant in integrating incoming information with contextual knowledge, which is particularly important in social cognition (Ames et al., 2015). Further, the DMN is specifically activated by processes of theory of mind, i.e. thinking about others, self-reference, i.e., thinking about oneself as well as in autobiographic memory and future planning (Spreng et al., 2009; Andrews-Hanna, 2012). The DMN is also involved in social processes such as social evaluations (i.e., judgments of social events and concepts), moral reasoning (i.e., pondering and determining how just or unjust an action seems to be), or social categorization (reflecting on social characteristics such as status and group phenomena) (Andrews-Hanna, 2012). In addition, the DMN is involved in storing memories and particularly in remembering autobiographic events and their greater context (Cabeza and St Jacques, 2007). Self-reference is a critical and defining feature of autobiographical memory (AM) (Brewer, 1986; Conway et al., 2005). Functional neuroimaging studies have shown that AM retrieval typically involves greater self-referential processes when compared to memory retrieval for stimuli encoded in the laboratory (for review Gilboa, 2004). Further, a quantitative meta-analysis of neuroimaging studies has shown high and consistent correspondence and hence extensive functional overlap between the four neurocognitive networks of AM, navigation, theory of mind, and default mode in the DMN (Spreng et al., 2009). Finally, the DMN has been found to contribute to story comprehension i.e., in the processing, understanding and remembering of narratives: Studies have shown that when people watch a movie (or as well read or listen to a story) areas that build the DMN were highly correlated with each other, but only in the case of comprehensible stories (Regev et al., 2013; Hasson et al., 2008; Lerner et al., 2011; Simony et al., 2016). Were the stories scrambled or are in a language the person does not understand these areas were not correlated (Simony et al., 2016). However, if the same story is presented to different people in different languages the DMN is shown to be correlated again (Honey et al., 2012). These studies suggest that the DMN is particularly associated with understanding the whole story, set it in a context and form the subsequent memory of it. Furthermore, not only the larger story line is likely processed in the DMN but the information is further set into context and analysed on a larger time scale. Ames et al., 2015 compared the inter-subject alignment of neural time courses when participants listen to auditory vignettes which were only comprehensible when they were presented together with valid contextual cues (Ames et al., 2015). Only in the case of valid (compared to invalid) contextual cues the significantly improved comprehension of the vignettes as well as neurally greater similarity between brain patterns in the midline core of the DMN was observed (Ames et al., 2015). When comparing the timescales of memory building from short (10–100 ms) to longer (several minutes) periods, responses with the longest processing timescales, at the apex of the hierarchy were found in areas of the DMN (Hasson et al., 2015). Therefore, we see several reasons to assume that the DMN is a particularly important structure in our study:

First, more similar brain activity patterns in the DMN could reflect similarity between sisters (more than for friends and acquaintances) for social and moral reasoning as e.g., a more uniform perception and evaluation of the moral dilemma. It can be assumed that the evaluation of the moral dilemmas (in case of genetic or adoptive sisters), involves a deep exploration of individuals' motives and how they relate to one's own values. These processes could be more similar in sisters than in

other relationship groups. Further, the social relevance of emotional stimuli could resemble more closely between sisters than between other study participants. Second, the memory of autobiographic events might be of particular importance in this study as sisters' memory may be more similar than the memory of friends and acquaintances. Even if the sisters memorize differently, they have memories about the same autobiographical events. Third, it is possible that sisters resemble in the comprehension of the movie: The movie depicts the moral dilemma of an organ donation and thus requires story comprehension as well as complex social processing and moral reasoning in particular. In a recent perspective paper, Yeshurun et al., (Yeshurun et al., 2021) state that the activity in the DMN is capable of both shaping other brains' responses and be shaped by the actions of other brains during social interaction. Further they found that the DMN is rather associated with meaning or action and invariant to changes in low-level perceptual properties. Thus, shared features as language, memories and schemas couple the DMN responses and allow to better align between people and thus this alignment might be particularly high between sisters. In the case reported here, the movie itself is also about a moral dilemma occurring between sisters. This fact could have strengthened the induction of similarity compared to the results reported above which were acquired with stimuli of other topics.

Further, when looking at the results of the ISFC analysis, it became apparent that the DMN was the network significantly connected with almost all other networks. This finding is not only in line with we know from other connectivity studies, with the default network being the core network between other subnetworks (Margulies et al., 2016), but further supports our findings in the ISC analysis: as the DMN has an essential role in multiple social interaction processes, it shows to be strongly activated and providing inter-brain connections in the relationships of particularly of sisters, as well as of friends and acquaintances.

#### 4.4. The empathy network

Further, activation in brain areas found in this study as e.g. the SPL, occipital and temporal cortex or the TPJ, has been associated with empathy-related neural resonance. Not only are these areas activated by processes of empathy but further their activation seems to be modulated by the emotional closeness between the examined participants. Specifically, Ionta et al., 2020 (Ionta et al., 2020) found that an event eliciting empathy (touch or pain induction) activate areas in the supramarginal gyrus (SMG) as well as anterior cingulum (ACC) stronger when the recipient of the event is felt to be emotionally close. Further, Wang et al. (2016) report that more cognitive attentional effort is needed for sharing a friends' pain while it takes less effort to judge a friends' happiness (compared to a stranger). Third, it has been shown that empathically strong events (compared with more neutral events) on a virtual body part which was felt as belonging to themselves (and therefore psychologically closer), elicit activity in TPJ (Pamplona et al., 2022). These finding might be interesting in the light of the relationship between homophily, empathy and emotional closeness. As the participants' ratings in respective questionnaires has shown, the emotional closeness both between friends and even more between sisters has been rated as very high. Thus, it seems plausible that at least in our study, homophily could be linked to the degree of emotional resonance. Given the correspondence of brain activity brain areas found in our study and the results reported above in the empathy network, one might postulate that empathy modulated by emotional closeness is a main driving factor for explaining the findings on homophily.

#### 4.5. Further brain activations

Beyond DMN and the empathy network, the sister's brain activity was higher correlated in the occipital and parietal cortices in the left and right hemisphere. Particularly, areas in both hemispheres' inferior and middle occipital cortices (IOG and MOG) on the lateral surface, as well

as the cuneus medially and the superior parietal lobule as well as the precuneus showed high ISC. While, as the stimulus is a movie, it is probable to assume that the involvement of the occipital areas represents visual processing, the higher correlation for sisters in these areas (compared to the other relationship groups) could be in addition based on processes linked to visual processes linked to social functions as e.g. in perceiving facial expressions (Foley et al., 2012) and emotion recognition (Lakis et al., 2011). Further, fMRI studies even showed involvement of the left occipital cortex in assigning person attributions (Kestemont et al., 2015) and observing violations of social norms (Berthoz, 2002). As the task in this experiment also requires considering social norms in the sense of asking if it is legit to make a difference of an organ donation between genetic and adoptive sisters, the relationship group of sisters as subjects could have more similar thoughts of social norms and thus a correlated brain activity in these areas. The cuneus has been associated with false belief and counterfactual reasoning in a social environment (Van Hoeck et al., 2014) which are equally relevant topics of the shown movie. The SPL in both hemispheres were also more strongly correlated in sisters than in friends and acquaintances. The SPL has multiple functions in social processing and has been shown (as the precuneus) to be an important area in theory of mind (Foley et al., 2012), emotion and moral processing (Harenski et al., 2008; Blair et al., 2007).

In the frontal cortex, the IFG, MFG and insula show higher ISC between sisters than between friends and acquaintances. These areas have been found to be involved in processing realistic social interaction scenarios (Fehr et al., 2014): more anterior distribution of activations is associated to motor-preparation and inhibitory control processing and activation in the insula is associated to pain- and/or aversion-processing for reactive-aggressive compared to social-positive scenarios. The authors anyway suggest common neural networks but also exclusive network parts depending on individual socialization for both sorts of social behavior. This insula particularly has been shown to be involved in pain empathy in general as well as for specific target groups (Azevedo et al., 2013).

As the individual socialization in a pair of sisters is likely to be more similar than between friends and acquaintances, the higher correlation could reflect a more similar processing in sisters in this aspect. A further frontal area showing higher ISC in sisters than in the other relationship groups is the (lateral) left frontal pole, which has been e.g. associated with self-reflection (Modinos et al., 2009).

When comparing the group of friends to acquaintances, correlated areas are sparser, but still the occipital and temporal cortex, namely the MOG/IOG, SOG, TPJ, MTG and precuneus, are higher correlated in friends than in acquaintances. As discussed above in detail, these areas have been involved in multiple functions of social processing, mentalizing and emotion and empathy processing. A similar reasoning as for the sisters may apply in a sense that friends show more similarity in the social functions associated with these areas than acquaintances, possibly as they resemble each other in their character, views, values opinions, interests, attitudes, beliefs and aspirations.

In a similar study conducted by Parkinson et al. (Parkinson et al., 2018), friends and three non-friend groups in increasing social distance were investigated in terms of neural similarity when viewing naturalistic stimulus. The existence of this study is providing us with the opportunity to compare results while also adding a novel social proximity level into the equation, which is kinship (i.e. in our study, sister pairs). Despite differences in analysis and parcellation methods, we have found compatible results with the aforementioned study within corresponding groups.

Parkinson's (Parkinson et al., 2018) study involves Distance 1 as friends group, and Distance 2 as friends of friends group which are corresponding to our Friends and Acquaintances groups. We are disregarding the later distance groups in Parkinson's study as we have not firmly established that the potential non-kin, non-friend and non-acquaintance subjects indeed share zero acquaintance with each

other (i.e. complete strangers). In terms of controlling independent factors, Parkinson study has demonstrated that gender and nationality were significant factors contributing to the social closeness whereas the age and other listed demographics were not; in our study as we have invited all female subjects with the same nationality but different ages, our subject pools are compatible for comparison in that they are free from the significant effects of tested independent variables.

Our analysis of the effect of social distance on neural similarity specifically highlighted brain regions were found to be those in the medial and lateral occipital cortex (i.e. calcarine gyrus, cuneus, and parts of the inferior, middle and superior occipital gyri), parietal areas (i.e. precuneus TPJ, ANG and SPL) and frontal areas (i.e. VMPFC, DMPFC, IFG and MFG). The brain areas showing correlation were not restricted to areas of basic perception, as e.g., low-level auditory and visual processing, typically activated during watching a movie, but correlations were also found in higher order associative areas. Parkinson's data highlights  $p > 0.01$  effect of social distance on neural processing similarity on specifically ventral dorsal striatum including nucleus accumbens, right caudate, left caudate, left putamen, right amygdala, right superior parietal lobe and left inferior parietal cortex. Therefore, in both studies, neural similarity in brain regions employed in sensory processing are found to be correlated with social proximity despite differing statistical analyses. The main difference between our study and Parkinson's is found to be the statistical significance of correlation between social proximity and frontal regions such as VMPFC and DMPFC. This might be explained by the fact that kinship has a distinct effect on emotional regulation and social judgment, especially considering that our experiment not only included sister pairs but also used a stimulus portraying a sisterhood situation. Our further analysis has found increased correlation in these brain regions in friend groups compared to acquaintance groups. Instead of prefrontal cortex involvement, Parkinson's study has demonstrated correlation with social proximity in ventral and dorsal striatum, amygdala, TPJ - areas which may be associated with emotional engagement and regulation.

Taken together, we found higher similarity of ISC in multiple brain areas when comparing sisters to either friends or acquaintances. Similarity in sisters could be due to genetic (inherited) similarity as well as due to similarities in their social environment. However, it has been shown that there is little evidence for the heredity of functional brain activity (BOLD signal) between siblings (see e.g. Côté et al., 2007). Genetic similarity may influence more processes than functional brain activity, e.g. it is possible that neurotransmission or connectivity resemble between sisters. As one aspect of similarity we examined here similarity of the gross brain anatomy between sisters and can report that elevated structural similarity in brain structure could be found in the present study (see Fig. 4), which might suggest that genetic similarity is not the exclusive reason of similarities that we have found between the similarities of functional brain activity between sisters. Further, the finding that also friends show more similar brain activity patterns than acquaintances, could not be explained with any genetic influence.

Further we could show that breathing and heart rate as well as the rating of valence and arousal were not significantly more similar between sisters than between other pairs. Rather, common up-bringing in the same family, sets the grounds for a high similarity in basic social factors (such as ethnicity, nationality, religion, social status and education) as well as further social factors as ties, tradition and practices, same heritage of religion, social status, values, and educational methods from their parents as well as shared memories. These factors may translate to the often very close emotional relationship between sisters sharing similar values, opinions, attitudes and beliefs and bear the potential to shape their conception of the world and thus the neuro-cognitive basis of their thoughts.

The excerpts of the movie "My sister's keeper" that we showed as stimulus is depicting a moral dilemma between the two sisters Anna and Kate. Anna is asked to donate a kidney to her sick sister but refuses to do so. Thus, the topic of this narrative focusing on the relationship between

two sisters by itself might have been intensified similarities between the sisters (and possibly friends, which were all female as well). Given that a) similarity has been shown as well for the pairs of friends (more as for acquaintances) and b) former work for friends as e.g. Parkinson et al., 2018 has shown similarity in brain activity using a set of movie clips (Parkinson et al., 2018), we would expect to still find higher inter-subject correlations of brain activity in sisters (compared with friends and acquaintances) when they watch movies of different content, not specifically thematizing a sisters' relationship. However, this assumption needs to be investigated for sisters in potential future studies.

#### 4.6. Conclusions

Our results also suggest a higher resemblance of brain activity patterns in friends than in acquaintances. In difference to the relationships between sisters, factors of genetics and common childhood in the same family cannot account for the found similarities. However, it has been shown that friends often share life circumstances and character traits and thus resemble in aspects as values, opinions, interests, intelligence, occupation, attitudes, abilities, beliefs and aspirations. Further, as friends a chosen voluntarily very likely based on communalities, one may assume that these similarities underlie the here found correlations of brain activity patterns. Finally, whereas acquaintances show basic similarities e.g., a similar perception of the audiovisual stimuli (movie), in the sensory cortices potentially reflecting universal processing present in all humans as well as further very basic similarities based on a similar social and cultural setting, the definitively lack the personal relationship that might underlie the more extensive similarity observed in friends and particularly in sisters.

Taken together, our findings show that sisters, beyond the simple perception of the stimulus, process and evaluate the events in the movie in a more similar way than subjects with a different relationship. The close resemblance in brain activity between sisters may be a result of common genes, although this possibility is not very likely, as within this study we controlled for the possibility that sisters have higher structural brain similarities. Overall, these results might partly help explain why more cognitive effort is exerted when thinking about friends than when thinking about kin (Włodarski and Dunbar, 2016), as higher similarity in how one perceives the world makes it less effortful to mentalize about kin than friends, and about friends than about acquaintances.

#### CRediT authorship contribution statement

**Mareike Bacha-Trams:** Writing – original draft, Visualization, Validation, Supervision, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Gökce Ertaş Yorulmaz:** Visualization, Software, Methodology. **Enrico Glerlean:** Visualization, Methodology, Data curation. **Elisa Ryyppö:** Visualization, Methodology. **Karoliina Tapani:** Methodology. **Eero Virmavirta:** Methodology. **Jenni Saaristo:** Methodology. **Iiro P. Jämskäinen:** Writing – review & editing, Supervision, Conceptualization. **Mikko Sams:** Writing – review & editing, Supervision, Conceptualization.

#### Declaration of competing interest

None of the authors claim any conflict of interest. None of the authors reports any competing financial interests.

#### Data availability

Unthresholded statistical parametric maps of this project can be found in neurovault: <https://neurovault.org/collections/ULZAPFRX/>. The code for the performed analysis is available at <https://github.com/eglerlean/sisterhoodfmri>.



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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.neuroimage.2024.120712](https://doi.org/10.1016/j.neuroimage.2024.120712).

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