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Social perspective-takingshapes brain hemodynamic activity and eye movements during movie viewing

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Abstract

Putting oneself into the shoes of others is an important aspect of social cognition. We measured brain hemodynamic activity and eye-gaze patterns while participants were viewing a shortened version of the movie 'My Sister's Keeper' from two perspectives: that of a potential organ donor, who violates moral norms by refusing to donate her kidney, and that of a potential organ recipient, who suffers in pain. Inter-subject correlation (ISC) of brain activity was significantly higher during the potential organ donor's perspective in dorsolateral and inferior prefrontal, lateral and inferior occipital, and inferior–anterior temporal areas. In the reverse contrast, stronger ISC was observed in superior temporal, posterior frontal and anterior parietal areas. Eye-gaze analysis showed higher proportion of fixations on the potential organ recipient during both perspectives. Taken together, these results suggest that during social perspective-taking different brain areas can be flexibly recruited depending on the nature of the perspective that is taken.

Key words: perspective-taking; neuroimaging; functional magnetic resonance imaging; inter-subject correlation; movie viewing

Introduction

Perspective-taking is an important aspect of human social cognition. To perceive and understand the world around us in a similar way is necessary for reaching a common ground and smooth communication. This involves both the physical environment and social situations between people. One possibility to achieve shared understanding of a situation is to adopt the same psychological perspective. By the process of social perspective-taking, the own point of view is temporarily suspended in order to simulate and view a situation from another person's different angle (Epley and Caruso, 2008).

Social perspective-taking requires building of an internal model or schema to be able to interpret the unfolding events, actions and interactions with task-relevant objects from the perspective of the other person. Social perspective-taking is a relevant factor in society as several studies indicate that it has a positive impact on social interactions and relations: perspective-taking can alleviate bias between groups (Todd *et al.*, 2012) and increases individuals' willingness to interact with out-group participants (Wang *et al.*, 2014), thus facilitating in-group/out-group exchanges (Galinsky and Moskowitz, 2000). Perspective-taking could also provide an advantage in different types of

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negotiations (Galinsky *et al.*, 2008). Further, perspective-taking could provide one important underlying mechanism for empathy, as one needs to put oneself in the position of someone else in order to feel the way he/she feels (Leong *et al.*, 2015).

Behavioural studies with participants sharing the same psychological perspective have shown that the interpretation of simple visual scenes (Kaakinen *et al.*, 2011) and the recall of expository text (Kaakinen *et al.*, 2002; Kaakinen *et al.*, 2003) are similar across individuals. Furthermore, it has been shown that both brain responses to specific objects in dynamic visual scenes and the related semantic categories are shaped by directing the participants' attention towards them (Çukur *et al.*, 2013). Similarly, attention may be directed to task-relevant sensory information when sharing a psychological perspective.

Furthermore, a distinction between cognitive and affective perspective-taking has been made before: while cognitive perspective-taking implies the ability to understand thoughts and beliefs of another individual, affective perspective-taking is focused on inferring another person's emotions and feelings. Brain imaging studies with functional magnetic resonance imaging (fMRI), using cartoons or written scenarios, have shown that the neural correlates of cognitive and affective perspective-taking are partly shared for both and involve brain areas as, e.g. temporoparietal junction and precuneus. Yet they also are dissociable from one another, with, e.g. cingulate cortex and limbic and basal ganglia structures uniquely involved in affective perspective-taking (Völlm *et al.*, 2006; Bodden *et al.*, 2013; Schlaffke *et al.*, 2015). In addition, differences were found within the frontal lobes between cognitive and affective perspective-taking: while cognitive perspective-taking elicited additional activation in the middle frontal gyrus, lateral orbitofrontal cortex, superior temporal gyrus and ventromedial prefrontal cortex (vmPFC), the medial orbitofrontal cortex was more strongly involved in affective perspective-taking (Hynes *et al.*, 2006; Sebastian *et al.*, 2012; Corradi-Dell'Acqua *et al.* 2014). Complementary findings of Kalbe *et al.* (2010), using transcranial magnetic stimulation applied to the right dorsolateral prefrontal cortex (DLPFC) to reduce cortical excitability when healthy male subjects performed a perspective-taking task, showed selective impairment of cognitive but not affective perspective-taking during the stimulation.

Developments in functional magnetic resonance imaging (fMRI) data analysis algorithms (Bartels and Zeki, 2004; Hasson *et al.*, 2004) have enabled investigation of socially complex interactions and their underlying neural correlates using movies as ecologically valid stimuli. Social stimuli tend to have ambiguous and convergent features that may be overlooked in isolated test settings. To overcome these limitations, many recent studies have successfully used rich stimulus environments to investigate perceptual brain functions with the aim of approaching the complexity of real life (e.g. Bartels and Zeki, 2004; Malinen *et al.*, 2007; Ylipaavalniemi *et al.*, 2009; Lahnakoski *et al.*, 2012). Greater sensitivity has also been shown in the clinical assessment of neuropsychiatric populations: impairment, e.g. in inferring an emotion from a static display of a facial expression, does not automatically have to translate into difficulty in interring emotions in real life, as the respective emotion in real life will co-occur with other behavioural cues (Fernandez-Duque *et al.*, 2010). These studies not only show the feasibility of such complex ecologically valid approaches (although recognising the obvious challenges in signal analysis due to the complexity of the recorded signals), but further indicate that using ecologically valid stimuli (in contrast to more standardised and less complex approaches) is particularly important in studies comprising multidimensional social interactions in order to make them as credible and perceptible as possible.

Thus, in this study, a movie was used as an ecologically valid stimulus during fMRI. The data were analysed using inter-subject correlation (ISC) of brain hemodynamic activity, which provides a model-free analysis approach and does not require any a priori model of the stimulus giving rise to the fMRI signal. In ISC the brains of individual subjects are aligned, and the correlations between the hemodynamic activity time courses for each voxel are calculated across all subject pairs, in order to examine the degree of similarity in individual brains' responses to the common movie stimulus. ISC can thus be interpreted as reflecting synchronised neural activity or similarity of cerebral information processing across individuals (Hasson *et al.*, 2004; Malinen *et al.* 2006; Wilson *et al.*, 2008; Kauppi *et al.*, 2010), solely based on similarities between the subjects' brain responses when they react to the various aspects of the complex stimulus (Hasson *et al.*, 2010). It has been shown with fMRI that during movie watching, not only basic sensory cortices but also 'higher-order' prefrontal cortical areas exhibit ISC of brain activity across participants (Jääskeläinen *et al.*, 2008; Hasson *et al.*, 2008). In addition, reliability and sensitivity of ISC to detect involved brain areas in complex experimental setups have been shown to be at the same level as in model-based analyses (Pajula *et al.*, 2012).

Similarities in how the brains of individual participants process the events in the movie, measured as ISC, may provide an important mechanism for similar information processing across study participants and form the basis of shared psychological perspective-taking. Therefore, ISC is particularly suited to examine social perspective-taking induced by movies. However, note that without any specific instructions on how to take perspective when viewing a movie, of course, the participants' similar viewing experience is based on how the movie director leads the viewer using techniques of cinematographic art (Hasson *et al.*, 2010).

One previous study investigating perspective-taking effects on brain activity used movie clips that the participants watched during fMRI (Lahnakoski *et al.*, 2014). Perspective-taking was observed to modulate brain activity in higher-order visual areas and inferior occipitotemporal areas. In this previous study, however, the participants adopted either a social perspective (forensic detective) or non-social perspective (interior decorator). It has not yet been addressed how taking two contrasting social perspectives, i.e. the perspective of one *vs* other movie protagonist in a drama movie, modulates information processing in the brain.

The present results were collected as a part of a larger dataset. We studied 30 participants watching a 24-min movie segment (modified from 'My sister's keeper' dir. Nick Cassavetes, 2009, Curmudgeon Films) during fMRI. The movie depicts a moral dilemma between two sisters. The protagonist Anna (potential organ donor) refuses to donate one of her kidneys to her sister Kate who is fatally ill from cancer (potential organ recipient). Due to Anna's refusal, Kate dies. In two previously published studies, two aspects of this dataset were analysed. In the first, the participants' brain activity patterns were compared when the participants assumed that the sisters were either genetic sisters or that the younger sister Anna had been adopted as a newborn (Bacha-Trams *et al.*, 2017). Analysing the ISC between participants in the two different conditions, this study showed significantly stronger correlations of brain activity patterns when the subjects believed that the sisters were genetically related particularly in the insula, cingulate, medial and lateral prefrontal, superior temporal and superior parietal cortices, thus areas which have been previously associated with processes such as moral and emotional conflict regulation, decision-making and mentalising. Although 90% of the subjects self-reported that genetic relationship was not relevant for the viewing experience, these results suggest that the mere knowledge of a genetic relationship between interacting persons modulated robustly the brain activity during film viewing.

In the second published study, we investigated how subjects with holistic and analytical thinking styles, as determined based on self-report questionnaire scores, differentially perceived the movie (Bacha-Trams *et al.*, 2018). In general, holistic thinkers are known to view background and objects more as a whole, by taking context into account, whereas analytical thinkers focus more on details such as perceptual objects at the expense of context. Holistic thinkers showed significant ISC in more extensive cortical areas than analytical thinkers, particularly in occipital, prefrontal and temporal cortices, suggesting that they perceived the movie in a more similar fashion, while in analytical thinkers, significant ISC was observed in right hemisphere fusiform gyrus, temporoparietal junction and frontal cortex.

In the present study, we analysed how adopting a social perspective of one or the other of the movie protagonists was reflected in the brain activity of the participants. These novel results were neither analysed nor reported in the two previously published studies.

Further, eye-gaze patterns and physiological responses (heart rate and breathing rate) were recorded during fMRI as the participants were viewing the movie. We hypothesised that there would be differences in eye-gaze patterns as well as in brain regions recruited, as indicated by differences in ISC, during the two perspectives. More specifically, as the two perspectives differ in their cognitive load, we hypothesised to find activations in brain areas associated with processing of moral dilemma, conflict monitoring and self-reflection during the perspective of the potential organ donor undergoing the moral dilemma (to donate an organ or not) and differentiable brain activity associated with empathy for the perspective of the sister suffering from terminal cancer. We further hypothesised that the subjects would prefer to watch the character whose perspective they were taking is disclosed by eye tracking.

Material and methods

Subjects

Thirty-three healthy female subjects (19–39 years, mean age of 26 years, one left-handed, laterality index of right-handed 84.5%) took part in this study, with none of the subjects reporting any history of neurological or psychiatric disorders. Further, all subjects had normal vision or wore contact lenses to obtain corrected-to-normal vision. The final analysis included 30 subjects, as three subjects had to be excluded due to discomfort in the scanner. Of these, 27 subjects were native Finnish speakers and three were native Russian speakers, but all subjects declared to be sufficiently proficient in English to follow the dialogue in the movie without subtitles. Female subjects were chosen for this study to make the identification with the female protagonists in the movie as easy as possible as the task consisted of watching a movie during fMRI that depicted a pair of sisters undergoing the moral dilemma of an organ donation. The study was carried out in accordance with the guidelines of the declaration of Helsinki (JAVA, 2013) and with the permission of the research ethics committee of the Aalto University (Lausunto 9 2013 Sosiaalisen kognition aivomekanismit, 8.10.2013), which also approved the experimental protocols. In addition, all subjects gave written informed consent prior to participation.

Stimuli and procedure

The results shown in this article were acquired as a part of a larger dataset. In the experiment, the subjects watched the feature film 'My Sister's Keeper' (dir. Nick Cassavetes, 2009, Curmudgeon Films), edited to 23 min and 44 s, with the main story line retained, during fMRI. This version of the movie depicts the moral dilemma of organ donation between the protagonists Anna (potential organ donor) and Kate (potential organ recipient). In the course of the movie, Anna refuses to donate and Kate dies. The reason for Anna refusing to donate the organ is revealed to the subjects after the experiment. The movie was shown to the subjects in the scanner on two different days. All subjects reported that they haven't seen the movie before. Each subject watched the movie four times (twice on each experimental day). For each viewing the instructions were varied: in addition to having the subjects to watch the movie from the perspective of the sister who was expected to donate the organ (potential organ donor Anna), and from the perspective of the potential organ recipient Kate, the subjects were asked to view the movie assuming either the sisters were related by birth or by adoption. The adopted *vs* genetic information always stayed fixed within a session, with each session consisting of taking once the perspective of the to-be-recipient and taking once the perspective of the to-be-donor sister (Figure 1). The order of the genetic *vs* adopted sessions and the perspectives within the sessions were counterbalanced across the subjects. Other aspects that resulted from this dataset, e.g. the differences between the conditions of genetic *vs* adoptive sisters as well as an investigation of the perception of the movie in participants with either holistic or analytical thinking, were reported in separate publications (Bacha-Trams *et al.*, 2017, 2018).

fMRI acquisition

Each subject was informed about the scanning procedures and asked to avoid bodily movements during the scans. The stimuli were presented to the subject with the Presentation software (Neurobehavioral Systems Inc., Albany, CA, USA), which was used to synchronise the onset of the movie stimuli with the beginning of the functional scans. The subjects viewed on a semi-transparent screen at 33–35 cm viewing distance via a mirror located above their eyes, where the movie was back-projected using a data projector (PT-DZ8700/DZ110X Series, Panasonic, Osaka, Japan). The movie was presented in the centre of the screen with approximate measures of 18 cm in width and 11 cm in height. The audio track of the movie, individually adjusted to be loud enough to be heard over the scanner noise, was played to the subjects with a Sensimetrics S14 audio system (Sensimetrics Corporation Malden, USA).

For scanning, a 3T Siemens MAGNETOM Skyra (Siemens Healthcare, Erlangen, Germany), at the Advanced Magnetic Imaging Centre, Aalto University, with a standard 20-channel receiving head-neck coil, was used. Anatomical images were acquired using a T1-weighted MPRAGE pulse sequence (TR 2530 ms, TE 3.3 ms, TI 1100 ms, flip angle 7°, 256×256 matrix, 176 sagittal slices, 1-mm3 resolution) and whole-brain functional data were acquired with T2∗-weighted EPI sequence sensitive to the BOLD contrast (TR 2000 ms, TE 30 ms, flip angle 90, 64×64 matrix, 35 axial slices, slice thickness 4 mm, 3×3 mm in plane resolution). For each movie viewing, a total of 712 whole-brain

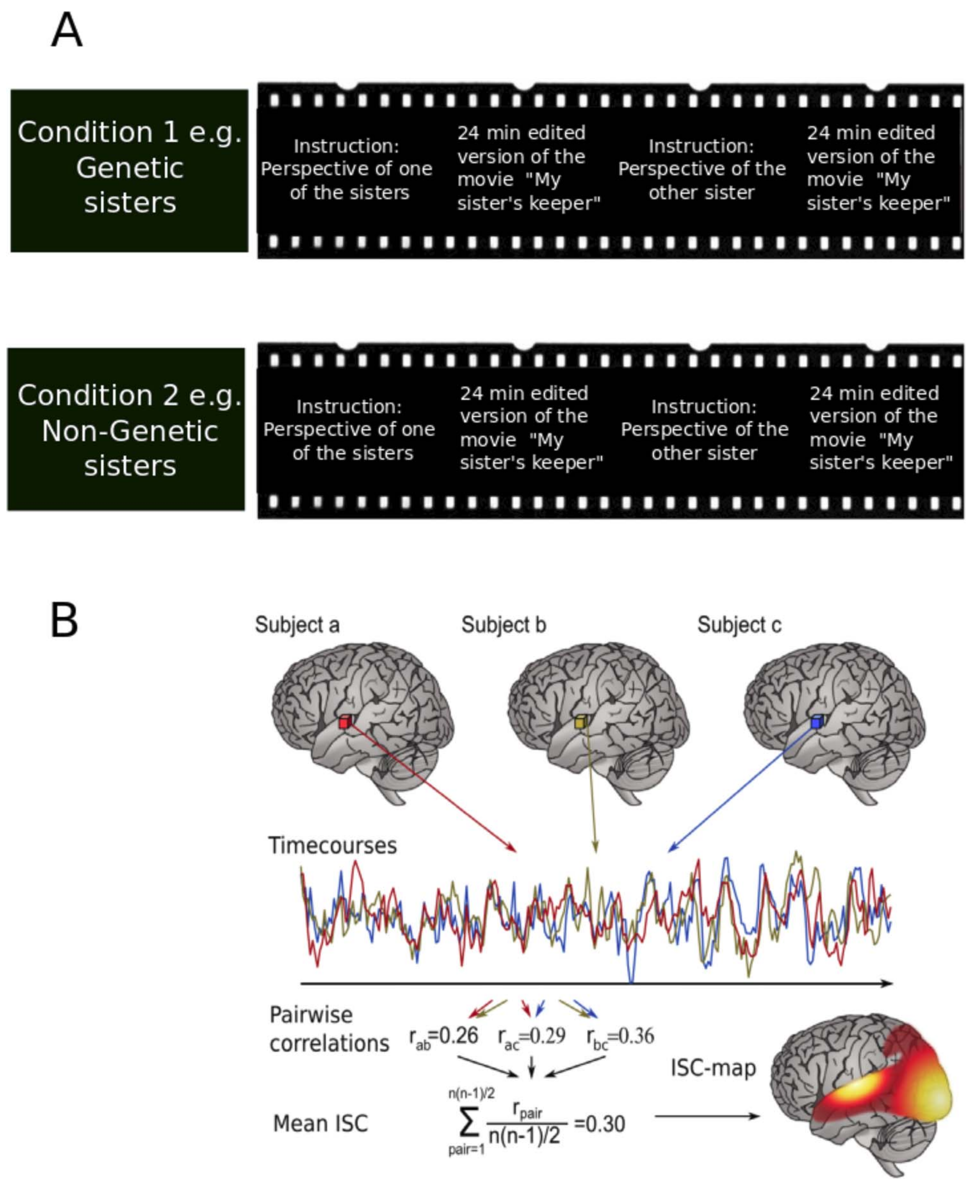

Fig. 1. Experimental procedure and ISC analysis in the movie viewing task [figure taken from Bacha-Trams *et al.* (2017)]. A: Participants viewed the same movie stimulus four times, in a 2 × 2 design, with believing that the movie characters are either genetically related or not as well as in the perspective of the to-be-donor sister Anna and in the perspective of the to-be-recipient sister Kate. The order of conditions was counterbalanced between participants. B: To obtain the mean inter-subject correlation (ISC), pairwise correlations across participants were calculated between the time series of each voxel from all the fMRI recordings. NB the ISC map in this figure is only for the purpose of illustrating the method.

EPI volumes were thus acquired. The Biopac system (Biopac Systems Inc., Isla Vista, California, USA) was used to monitor heart pulse and respiration during fMRI. Instantaneous values of heart rate and breathing rate were estimated with Drifter software package (Särkkä *et al.,* 2012) (http://becs.aalto.fi/en/research/bayes/drifter/).

fMRI preprocessing

For fMRI preprocessing standard steps were applied using the FSL software (www.fmrib.ox.ac.uk) and custom MATLAB code (available at https://version.aalto.fi/gitlab/BML/bramila/). Briefly, EPI images were corrected for head motion using MCFLIRT. Further, in a two-step registration procedure using FLIRT, the EPI images were co-registered to the Montreal Neurological Institute 152 2 mm template: from EPI to subject's anatomical image after brain extraction (9 degrees of freedom) and from anatomical to standard template (12 degrees of freedom). Spatial smoothing was applied with a Gaussian kernel of 6 mm full width at half maximum, and a high pass temporal filter at a cut-off frequency of 0.01 Hz was used to remove scanner drift. To clean the BOLD time series from deep white matter, ventricles and cerebral spinal fluid locations in order to further control for motion and physiological artefacts, 24 motion-related regressors were used (see citation Power *et al.,* 2014 for details, cerebral spinal fluid mask from SPM8 file csf.nii, white matter and ventricles masks from Harvard Oxford atlas included with FSL). Displacement of instantaneous head motion was framewise computed as a measure of quality control: 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 suggested in Power et al. (2012). For the remaining three runs, the number of time points under 0.5 mm was 639 (89.7%), 633 (88.9%) and 489 (68.7%), i.e. only one session had a considerable amount of head motion. This session was removed from the dataset. During across-brain time series correlation, head motion is expected to reduce the SNR. To be sure that head motion similarity did not explain any group difference, the same permutation test as for the ISC was also computed for average framewise displacement by estimating the similarity of two subjects as the distance between their average framewise displacement value. The similarity in average head motion was not different between the two viewing conditions ($t = 0.255$; $P = 0.398$ obtained with 5000 permutations).

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

To examine the similarity of brain activity 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). In the toolbox, for each voxel a similarity matrix is computed between subject pairs and within the same subject in all conditions, with the conditions being (i) shared perspective of the to-be-organ-donor, (ii) shared perspective of the to-be-organ-recipient, (iii) shared assumption that the movie's sisters are genetically related and (iv) shared assumption that the younger sister was adopted. The total size of the similarity matrix is then 120×120 (4 conditions $\times$ 30 subjects), with each subject having two viewings in the perspective of the potential organ donor Anna and two viewings in the perspective of the potential organ recipient Kate. The comparison between the conditions in the two perspectives results thus in a total of 1740 pairs per condition, as the similarity of BOLD time series during the two viewings (in each perspective) of each subject is compared with the two respective viewings of the other $N - 1$ subjects. As the order of subjects does not matter, the final number of pairs in same conditions will be $2*2*(N-1)*N/2 = 1740$ with $N = 30$.

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. The differences between experimental conditions are computed by first transforming the correlation values into z-scores with the Fisher Z transform and then computing t-values and corresponding P-values using a permutation-based approach (Glerean et al., 2016).

The Fisher Z-transformed correlations of the either the genetic or the non-genetic sisterhood were pooled for the two perspectives.

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 as correction for the multiple comparison. Further, for visualisation purposes, cluster correction with removing any significant cluster smaller than $4 \times 4 \times 4$ voxels was performed, 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/4092/.

Recording of eye movements

During fMRI scanning, eye movements were recorded from all subjects with an EyeLink 1000 eye-tracker (SR Research, Mississauga, Ontario, Canada; sampling rate 1000 Hz, spatial accuracy better than 0.5°, with a 0.01° resolution in the pupil-tracking mode). The measurement comprised 120 recordings (30 subjects with 4 sessions each) (conditions: genetic and perspective of the potential organ donor Anna, genetic and the perspective of the potential organ recipient Kate, adopted and the perspective of the potential organ donor Anna, adopted and the perspective of the potential organ recipient Kate). Due to technical problems, 59 out of the 120 had to be excluded from the final data analysis, with the rejection criteria of blinks at a maximum of 10% of the duration of the scan and a majority of blinks and saccades of less than 1 s in duration. These data comprised full datasets of 3 subjects as well as parts of the datasets of 23 other subjects (in 4 subjects not any of the recorded files passed the quality control), resulting in 61 recorded files with sufficient quality (see Supplementary Table S1 for details). The two perspectives were almost equally presented among the accepted files: 31 files were from sessions with the potential organ donor Anna's perspective and 30 with the sick sister Kate's perspective (further, from the 61 accepted files with sufficient quality, 27 were recorded in the genetic condition and 34 in the adopted condition) (see Supplementary Table S1 for the exact files). As not every subject had recordings passing the quality control for both perspectives in either the condition of genetic or adopted relationship, only 24 pairs could be built for the perspective comparison (see Supplementary Table S1).

The eye-tracker was calibrated once with a nine-point calibration prior to the experiment. As the experiment was relatively long and no intermediate drift correction was performed, we retrospectively corrected the mean effect of the drift. For that purpose, first the mean of all fixation locations over the entire experiment for each subject was calculated, and then the fixation distributions were rigidly shifted so that the mean fixation location coincided with the grand mean fixation location over all subjects. Saccade detection was performed using a velocity threshold of 30°/s and an acceleration threshold of 4000°/s2. Events above the threshold were regarded as a saccade; events below the threshold were regarded as a fixation.

Eye movement analysis

Subject-wise gaze fixation distributions were compared across the two perspectives. For that purpose, we generated individual heat maps by modelling each fixation as a Gaussian function using a Gaussian kernel with a standard deviation of 1 degree of visual angle and a radius of 3 standard deviations. Corresponding to the TR used in the fMRI measurements, these heat maps were generated in time windows of 2 s.

Spatial similarities were calculated between each pair of heat maps across eye-tracking sessions using Pearson's product–moment correlation coefficient (Nummenmaa et al., 2014). In the end a similarity matrix was obtained with correlations between each pair for each of the 712 time windows.

The mean ISC for eye-gaze patterns (eISC)

The mean eISC scores over all 712 time windows were examined by first extracting the mean of Fisher's Z-transformed correlation scores and then transforming these mean values back to the correlation scale before the statistical analysis. The statistical significance was calculated between three different groups: (i) the same perspective of Anna, both participants are in the perspective of the potential organ donor Anna (465 pairs); (ii) the same perspective of Kate, both participants are in the perspective of the potential organ recipient Kate (435 pairs); and (iii) different perspectives, one participant is in the perspective of Anna and the other one in the perspective of Kate (930 pairs). In order to avoid making assumptions about the data distribution, non-parametric permutation tests with a total of 100 000 permutations were used. In the permutation test, the data labels were mixed randomly in order to change the groupings of the data and to observe the resulting differences in the means of these randomised new groups. The final P-values for the statistical significance were acquired from this estimated distribution by observing how many of the permuted random partitions into groups yielded a more extreme group mean difference than the one observed with the original grouping.

Region of interest analysis

In eye-tracking region of interest (ROI) analysis, specific regions are chosen on the stimulus screen to cover objects or targets that are assumed to interest the subjects visually (Nummenmaa *et al.,* 2014); in this study, the two protagonists were chosen to be the ROIs. Thus, in each of the 35 614 frames of the movie, the locations of the potential organ donor Anna and the potential organ recipient Kate were marked on the stimulus screen by drawing polygons around each protagonist. As the movie was shown in the centre of the screen (see Methods above), the viewing angle for both ROIs was comparable. The polygons were of comparable size for both of the protagonists in average. Logical matrices with zeros and ones were generated for each frame by marking as ones these pixels that were covered by the polygon. Then, the fixations of each participant were analysed by testing if the participant had viewed one of the ROIs in each frame, i.e. if the fixation lay within the polygon area marked with ones in the matrices.

Two different metrics were calculated: (i) the overall viewing and (ii) the preference. The overall percentage was defined as the time that the subject was viewing each ROI of the time when that ROI was present on the screen. The overall percentage was calculated for each viewing session as follows:

$$\text{The overall viewing\%} = \frac{\text{The No.of frames where the subject views the ROI}(i)}{\text{The No.of frames where the ROI}(i)\text{ is present}}$$

where $i = \{\text{Anna, Kate, Both}\}$.

This overall percentage (%) was calculated for fixations on the potential organ donor Anna and the potential organ recipient Kate separately. In addition, as there was an occasional overlap between the ROIs when the protagonists were close to each other on the screen, an option of fixating on both was examined.

The overall viewing was examined between perspectives, as well as within a perspective. For the within perspective comparisons, the pairing was formed automatically because the comparisons were done between the fixations on Anna and Kate in the same session. However, in the between perspective comparison, the same participant's eye-tracking sessions recorded on the same day with the same knowledge of the genetic or non-genetic bond between protagonists were compared in order to have the perspective as the only differing variable. An appropriate pairing of sessions was not possible for all 61 acceptable eye-tracking files, but only for 24 pairs of viewing sessions (see Supplementary Table S1), which were analysed in the final testing. In these pairs, a dependent Wilcoxon rank sum test was used to test for between perspective differences. Separate tests for the fixations on Anna, Kate and both protagonists were used, resulting in three different P-values (fixations on Anna, fixations on Kate or fixations on both ROIs simultaneously).

To analyse the differences within perspective, dependent Wilcoxon rank sum tests were used by pairing the fixations on Anna and Kate in the same session, with 31 viewing sessions from the potential organ donor Anna's perspective and 30 sessions from the potential organ recipient Kate's perspective. While the overall viewing for each ROI was used to measure if the subject is fixating on the ROI when visible in the movie, the preference gave a measure of the participants' choice to favour one of the ROIs when both were present in the movie frame. The preference (%) was obtained by examining only the frames where both of the ROIs were present in the stimulus screen. The preference was calculated by analysing how often the subject was fixating on each ROI during these frames.

$$\text{The preference\%} = \frac{\text{Both ROIs present AND the subject views the ROI}(i)}{\text{The No.of frames where both ROIs present}}$$

where $i = \{\text{Anna, Kate}\}$.

The preference analysis was based only on fixations on the potential organ donor Anna and the potential organ recipient Kate, as fixations on both did not contain meaningful information in the context of favouring one of the protagonists. These kinds of frames were included both in the preference percentage of Anna and Kate.

The statistical analysis of the preference percentage was conducted the same way as for the overall viewing percentage. For between perspectives comparison, the dependent Wilcoxon rank sum test was used with 24 pairs. However, in contrast to the overall viewing analysis, here only the percentages of Anna and Kate were examined as the preference percentage was not meaningful for the fixations on both protagonists simultaneously (resulting in two P-values). For between perspectives comparison, dependent Wilcoxon rank sum tests were used by pairing the fixations on Anna (30 sessions as above) and Kate (30 sessions as above).

Behavioural measurements

Behavioural questionnaires. After the first fMRI session, the participants were asked about their perception of the movie in five short free-form questions. The questions specifically asked e.g. 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 end of the fMRI measurement, after the fourth movie viewing (on the second experimental day), the participants viewed the ending of the original movie to debrief them. The ending reveals that the potential organ recipient Kate had wished for the healthy sister to refuse donating her kidney. After seeing the real ending, the participants were asked if now they changed their opinion on the roles of the two movie protagonists.

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 (Hatfield *et al.,* 1994) and the BIS/BAS scale (Carver and White, 1994). Hatfield's Emotional Contagion Scale measures contain 18 questions that are answered using a 4 point Linkert scale, resulting in a score between 18 and 72. The BIS/BAS scale uses four 5 point Linkert subscales to measure (i) the behavioural inhibition system (BIS), as well as the behavioural activation system with the aspects (ii) BAS Drive (motivation to

Table 1. Peak coordinates of ISC clusters for each perspective

Cluster ID	Cluster size	x	y	z	Max t-value
Positive clusters (perspective of the potential organ donor Anna)					
Inferior occipital cortex (L)	2934	−30	−84	−12	9.80
Middle temporal gyrus (L)	240	−52	2	−30	7.90
Temporal pole (L)	197	−50	22	−12	8.13
Superior frontal gyrus (R)	170	20	42	30	5.62
Superior parietal lobule (R)	167	12	−58	64	6.19
Cerebellar lobe VIIIb (L)	149	−14	−42	−54	6.30
Superior temporal gyrus (R)	135	50	−6	−10	7.45
Middle temporal gyrus (L)	131	−18	46	24	6.72
Positive clusters (perspective of the potential organ recipient Kate)					
Middle temporal gyrus (R)	427	58	−44	2	−8.51
Heschl's gyrus (L)	206	−30	−26	14	−7.01
Cerebellar crus II (L)	189	−16	−72	40	−6.93
Middle temporal gyrus (L)	173	−60	−56	14	−6.14
Superior temporal gyrus (R)	151	58	−34	20	−5.93
Cerebellar lobe VIIb (R)	149	24	−70	−46	−6.72

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). The BIS/BAS questionnaire contains 24 questions, with 7 questions belonging to the BIS score, 4 questions for the BAS Drive subscale, 4 questions for the BAS reward responsiveness subscale, 5 questions for the BAS fun-seeking subscale and 4 fillers. Thus, possible scores lie between 7 and 35 for the BIS subscale as well as 5–25 for BAS Drive and BAS fun seeking and 4–20 for BAS reward responsiveness. Further, each participant quantified her social network (Roberts and Dunbar, 2011), including their emotional closeness to the mentioned individuals. The scores from the questionnaires were compared to the ISC of brain activity using a conjunction analysis. Dissimilarity matrices between each subject pair were calculated for the seven factors (Hatfield's Emotional Contagion Score, Hatfield's Emotional Contagion Scale, BIS scale, BAS drive, BAS fun seeking, BAS reward responsiveness as well as the social network size) and compared to the dissimilarity matrices of ISC between subject pairs.

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 analysed and published separately (Bacha-Trams *et al.*, 2018).

Analysis of behavioural measurements

Heart rate and breathing rate analysis. Heart and breathing rate were recorded during fMRI and analysed 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 two perspectives of the potential organ donor Anna and the potential organ recipient Kate were computed in the same way as in the ISC analysis: first, correlation values were transformed into z-scores with Fisher Z's transform, and then a permutation-based approach was used to compute *t*-values and corresponding P-values. Correction for the multiple comparisons was performed with Benjamini–Hochberg false discovery rate (BH-FDR) correction at a $q < 0.05$, corresponding to a *t*-value threshold of 2.133.

Results

Inter-subject correlation in fMRI

In this study, the ISC and eye tracking of 30 female subjects were examined when they watched a feature movie. The subjects were asked to take either one or the other perspective in the movie depicting two sisters as protagonists, with one being asked to donate an organ for the other. The subjects should take the perspective of the potential organ donor Anna in one experimental condition and the perspective of the potential organ recipient Kate in another experimental condition. In addition to taking a perspective, the subjects were asked to watch the movie assuming that the sisters were either genetic sisters or that the younger sister was adopted. The movie was watched under four different conditions: (i) the subjects took the perspective of the potential organ donor Anna thinking that the sisters had a genetic relation, or (ii) they took the perspective of Anna assuming she was adopted as a newborn. Further, each subject viewed the movie in the perspective of the potential organ recipient Kate, assuming either (iii) genetic relation or (iv) adoption. The order of the experimental conditions was counterbalanced between the subjects, and the effects of the order were checked. The analysis revealed that the first presentation of the movie always elicited the strongest ISC, but as all conditions of each subject was compared to all conditions of another, with counterbalanced order of experimental conditions, the effect was balanced out. All results of the aspect of their movie protagonists' relationship to be genetic or adopted are reported at Bacha-Trams *et al.* (2017).

Table 1 and Figure 2 show the brain regions with significantly higher ISC during the perspective of potential organ donor Anna (warm colours in the figure) and the opposite contrast, significantly higher ISC during the perspective of the potential organ recipient Kate (cold colours), calculated as voxel-wise means of pairwise ISC of participants within each group. During the perspective of the potential organ donor Anna, higher ISC was found in the left hemisphere dorsal–frontal area, insula, temporal pole, angular gyrus, cuneus, lateral occipital, medial occipital cortex and posterior cingulate cortex (PCC) and in the right hemisphere dorsal–frontal area, inferior frontal gyrus (IFG) and insula, medial occipital cortex including fusiform gyrus and in the right amygdala. For the perspective of the potential organ recipient Kate,

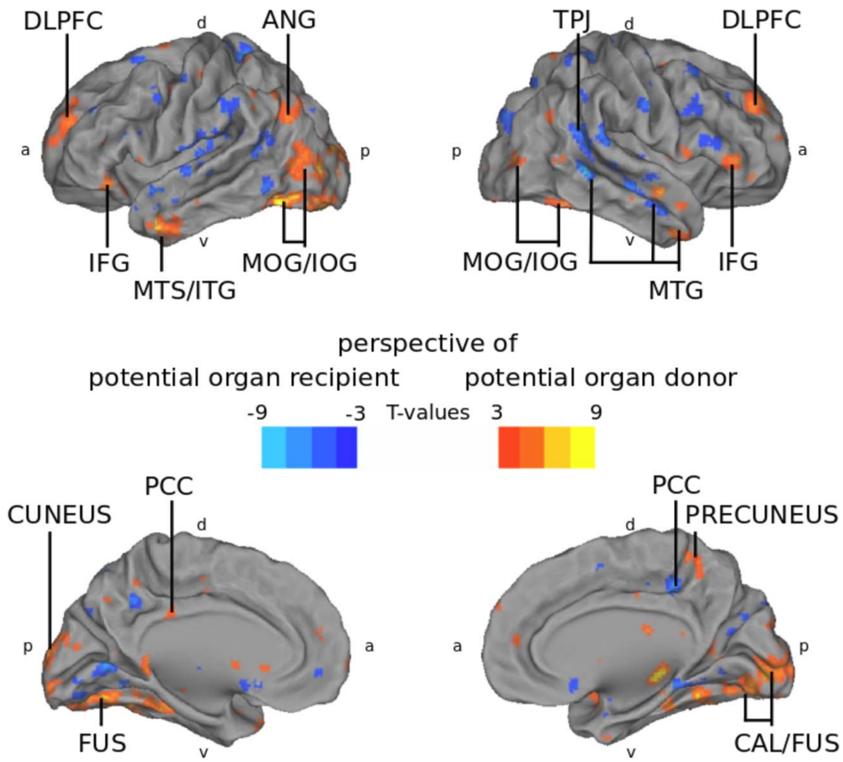

Fig. 2. Results of an ISC contrast between the two perspective conditions, with warm colours showing significantly higher ISC when the participants assumed the perspective of the potential organ donor Anna and cold colours showing the perspective of the potential organ recipient Kate.

there were several areas showing higher ISC in posterior lateral–frontal, superior temporal and parietal cortical areas. While the significant differences in ISC between the perspective conditions were observed across a number of cortical regions, there were some clear differences in each of the lobes. In the prefrontal cortex, assuming the perspective of the potential organ donor, significantly higher ISC was elicited in more anterior areas, and assuming the potential organ recipient perspective, significantly higher ISC was elicited in more posterior areas. In the temporal lobe, assuming the perspective of the potential organ donor, significantly higher ISC was elicited in more superior middle areas, including auditory cortical areas, and assuming the potential organ recipient perspective, significantly higher ISC was elicited in ventral anterior and ventral posterior areas. In the parietal lobe, taking the perspective of the potential organ donor, significantly higher ISC was elicited in more posterior areas, and assuming the potential organ recipient perspective, significantly higher ISC was elicited in more anterior areas, including somatosensory cortical areas. Lateral occipital areas were showing higher ISC in the perspective condition of potential organ donor, whereas in the medial occipital cortex, there were also areas showing higher ISC in the potential organ recipient condition. Overall then, in the potential organ recipient condition, significantly higher ISC was observed in sensory areas, and in the potential organ donor condition, significantly higher ISC was observed in higher-order areas.

Eye tracking

The mean ISC for eye-gaze patterns (eISC)

Further, eye-gaze patterns were recorded during watching the movie from both perspectives for each participant. In the temporal ISC for eye-gaze pattern analysis (eISC) across the whole movie, the eISC differed in 50% (357 out of 712 time windows) of all time points significantly between the perspectives (Figure 3). In 60% of the significantly different time windows, the mean temporal eISC was higher in participants taking the potential organ donor Anna's perspective than in participants taking the perspective of the potential organ recipient Kate. During the movie, there are scenes showing (i) both characters in the frame, (ii) only one of the characters or (iii) neither of the characters. However, as the proportions of the time the protagonists were present separately, together or not at all were approximately the same (for all the time windows, as well as for the time windows with significant group differences), the differences in eye-gaze patterns were not likely simply due to the differences in the presence or absence of the protagonists.

eISC within and across perspectives. Further, a comparison was made, for the general eISC contrasting participants being in the same perspective (i.e. where both participants were taking the perspective of the potential organ recipient Kate or that of the potential organ donor Anna) *vs* participants across perspectives (i.e. where one of the participants was taking the perspective of the potential organ recipient Kate and one of the potential organ donor Anna). When contrasting the movie viewings with both participants taking the same perspective against cross-perspective pairs, higher correlations were observed between participant pairs taking the perspective of the potential organ donor Anna as compared to cross-perspective pairs ($P < 0.01$, difference in means 0.053). In contrast, the eye-gaze patterns of pairs both taking the perspective of the potential organ recipient Kate did not yield significantly higher correlations compared with the cross-perspective pairs ($P = 0.3168$ difference in means 0.007). Similarly, differences were not statistically significant

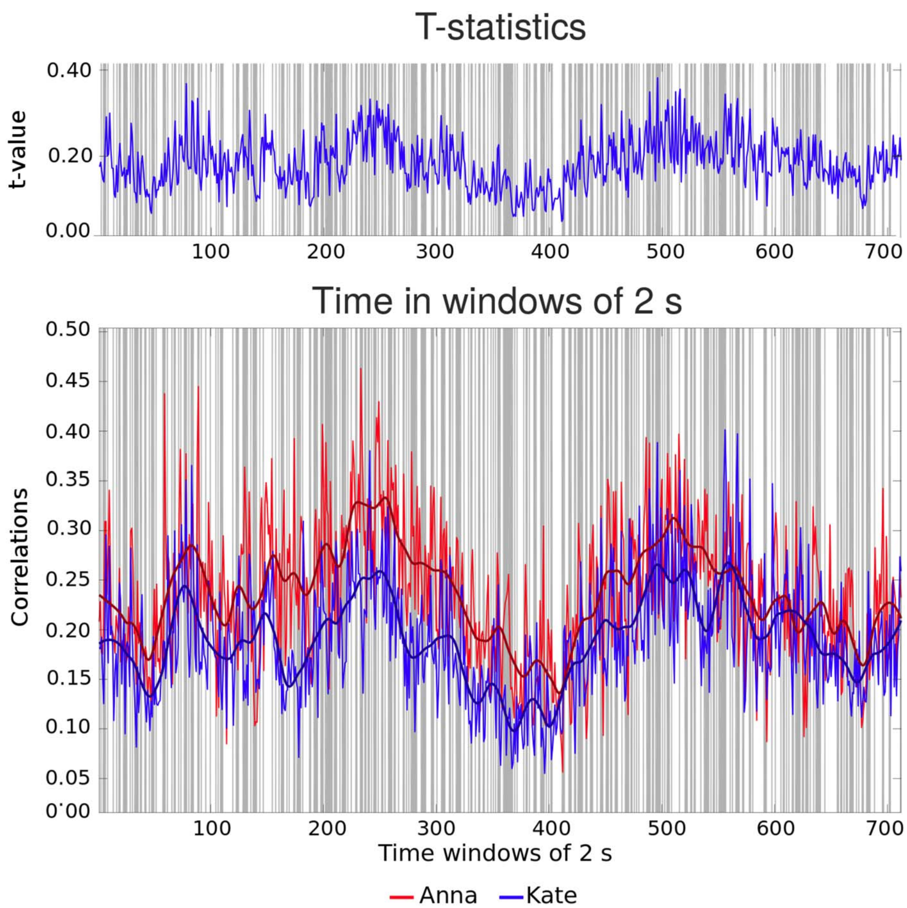

Fig. 3. The temporal eISC results. Time windows with significant between-perspective differences are marked in grey.

when directly contrasting the participant pairs when following the potential organ donor Anna with the pairs of participants when taking the perspective of the potential organ recipient Kate ($P = 0.0936$, difference in means 0.046). These results are illustrated in Figure 4 (group means for both subjects taking the perspective of Anna = 0.239, s.d. = 0.159, group means for both subjects taking the perspective of Kate = 0.193, s.d. = 0.128, group means for subjects across perspectives = 0.187, s.d. = 0.128).

Region of interest analysis

Overall viewing percentage and viewing preference. In addition to the general eISC analysis, an eye movement analysis was carried out to determine differences in perspective-taking only in the scenes when either both or one of the two movie characters was visible in the movie frame (i.e. excluding scenes with none of the movie characters shown). Two factors were considered: the overall viewing behaviour, i.e. in how many frames of the movie that show the protagonist she is fixated by the subject, and the viewing preference, i.e. in how many frames showing both movie protagonists is either the potential organ donor Anna or the potential organ recipient Kate fixated and thus 'preferred' over the other visible at the same time.

Further, the comparisons were done both between and within perspective-taking conditions in separate analysis. Thus, from all scenes showing at least one of the characters, the percentage to watch either the potential organ donor Anna or the potential organ recipient Kate was calculated for each participant in each perspective.

Between perspectives. For the analysis between perspective-taking conditions, the overall viewing percentage as well as the preference for a protagonist was calculated between participants who took the perspective of the potential organ donor Anna and the potential organ donor recipient Kate. Both analyses showed differences in the viewing behaviour, depending on which one of the two perspectives the participant was taking. The participants taking the potential organ donor Anna's perspective watched the movie character Anna more in the analysis of the overall viewing percentage ($P = 0.007$, pairs Anna median = 0.350, median absolute deviations (MAD) = 0.101, pairs Kate median = 0.220, MAD = 0.045), and they showed a significantly larger preference percentage for Anna ($P = 0.0086$, pairs Anna median = 0.152, MAD = 0.080, pairs Kate median = 0.099, MAD = 0.030) (Figure 5). Interestingly, the participants in the potential organ donor (Anna's) perspective viewed the potential organ recipient Kate more than the participants taking Kate's perspective. This was not statistically significant in the overall viewing percentage ($P = 0.153$, pairs Anna median = 0.400, MAD = 0.106, pairs Kate median = 0.253, MAD = 0.053) but significant in the preference analysis ($P = 0.022$, pairs Anna median = 0.228, MAD = 0.054, pairs Kate median = 0.165, MAD = 0.036) (Figure 5).

Within perspectives. In the analysis of within perspective-taking conditions, it was determined if, when taking the same perspective (either both the perspective of the potential organ donor Anna or the potential organ recipient Kate), the

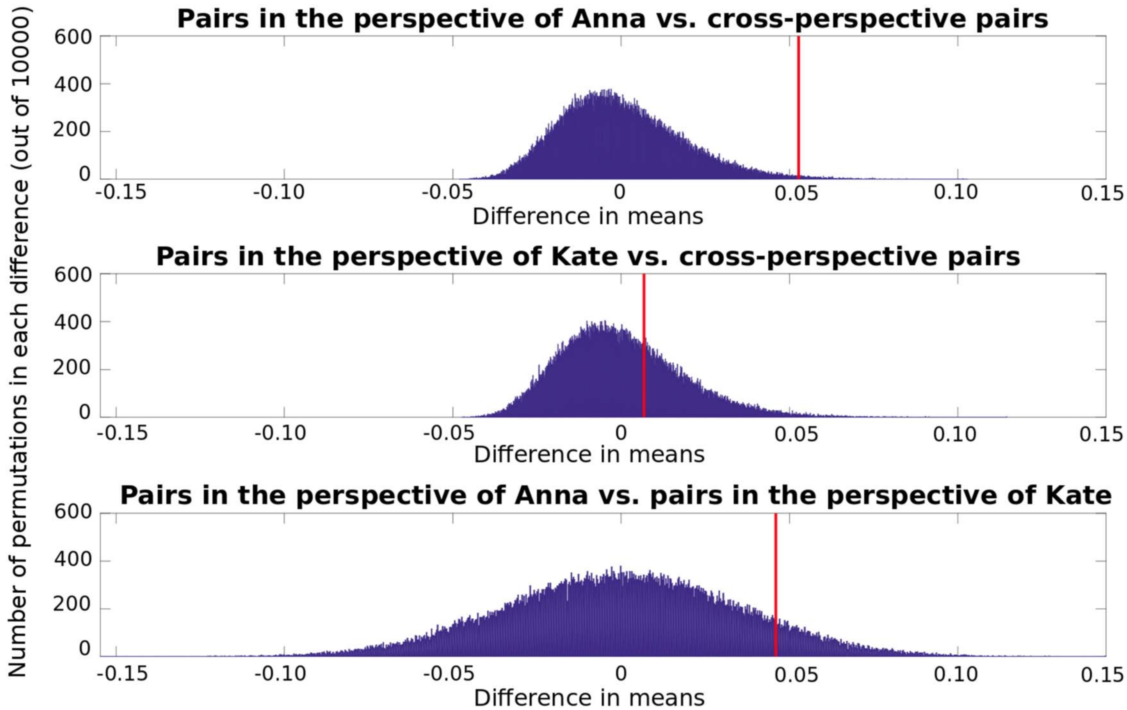

Fig. 4. Permutated distributions for the differences in group means for the analysis of mean eISC over the movie. Observed differences are marked in red.

participants watched the protagonist Anna more than Kate or vice versa. For both groups, the participants in the perspective of the potential organ donor Anna and the participants in the perspective of the potential organ recipient Kate preferred to watch Kate in both the overall viewing percentage and the preference between the movie protagonists (Anna's perspective overall viewing percentage: $P = 0.001$, pairs Anna median = 0.295, MAD = 0.091, pairs Kate median = 0.386, MAD = 0.101, preference percentage: $P = 0.0006$, pairs Anna median = 0.143, MAD = 0.070, pairs Kate median = 0.218, MAD = 0.048, Kate's perspective overall viewing percentage: $P = 0.8 \times 10^{-5}$, pairs Anna median = 0.224, MAD = 0.053, pairs Kate median = 0.271, MAD = 0.064, preference percentage: $P = 0.2 \times 10^{-5}$, pairs Anna median = 0.099, MAD = 0.032, pairs Kate median = 0.172, MAD = 0.040) (Figure 6).

Physiological measurements

The physiological measurements of heart and breathing rate, recorded to examine if there were differences between the movie watching conditions or if any correlation between the heart and breathing rate and other measures of the study could be found, did not differ between the two perspective groups (with bootstrap over 5000 permutations heart rate: t-test, $t = -0.5400$, $P = 0.7022$; breathing rate: t-test, $t = -0.6977$, $P = 0.7545$), neither did they specifically correlate with either ISC or eye tracking. Likewise, no significant difference could be found in the heart and breathing rate comparing the conditions of assumed genetic *vs* non-genetic sisters (with bootstrap over 5000 permutations, breathing rate: group means for the perspective of Anna = 0.022, s.d. = 0.067, group means for the perspective of Kate = 0.025, s.d. = 0.068: t-value = −1.12, $P = 0.262$, heart rate: group means for the perspective of Anna = 0.013, s.d. = 0.078, group means for the perspective of Kate = 0.012, s.d. = 0.078, t-value = 0.430, $P = 0.666$).

Behavioural measurements

Behavioural questionnaires. Analysis of the free-form questions showed that, based on their own self-evaluation, the subjects were successfully able to take either of the two perspectives. While 6 subjects reported that it was equally easy to take the perspective of the potential organ donor Anna and the potential organ recipient Kate, 10 found it easier to take the position of Kate and 14 found it easier to take the perspective of Anna. The main reason for considering Kate's perspective as easier was that she had a more passive role and was not being in the dilemmatic decision, while the main reasons finding it easier to take Anna's perspective were that the story was depicting her dilemma and decision and that subjects reporting her perspective as easier have, as Anna, an older sister in real life. Further, a majority of subjects (90%) reported that their evaluation of the two movie characters changed after they were debriefed with the original ending of the movie after the last scanning session. (The debriefing had thus no effect on the scans under the different conditions.) Further the questions revealed that 90% of the subjects would donate an organ to her sister if there would be in such a situation (and 90% reporting that in this case it would not make a difference to them if the sister was a genetic or an adopted sister.)

Social network questionnaires. In the social network questionnaire (Roberts and Dunbar, 2011), the subjects quantified their social network with mentioning all persons they consider having a relationship with (all living relatives regardless of the relationship, as well as friends, with whom they had contact over the last 12 months). The average social network size lays at 70.5 (s.d. = 32.0 ranging from 10 to 134 mentioned persons), with 27.6 family members in average (s.d. = 9.6 ranging from 6 to 46) and 35.0 friends in average (s.d. = 22.3, ranging from 4 to 95).

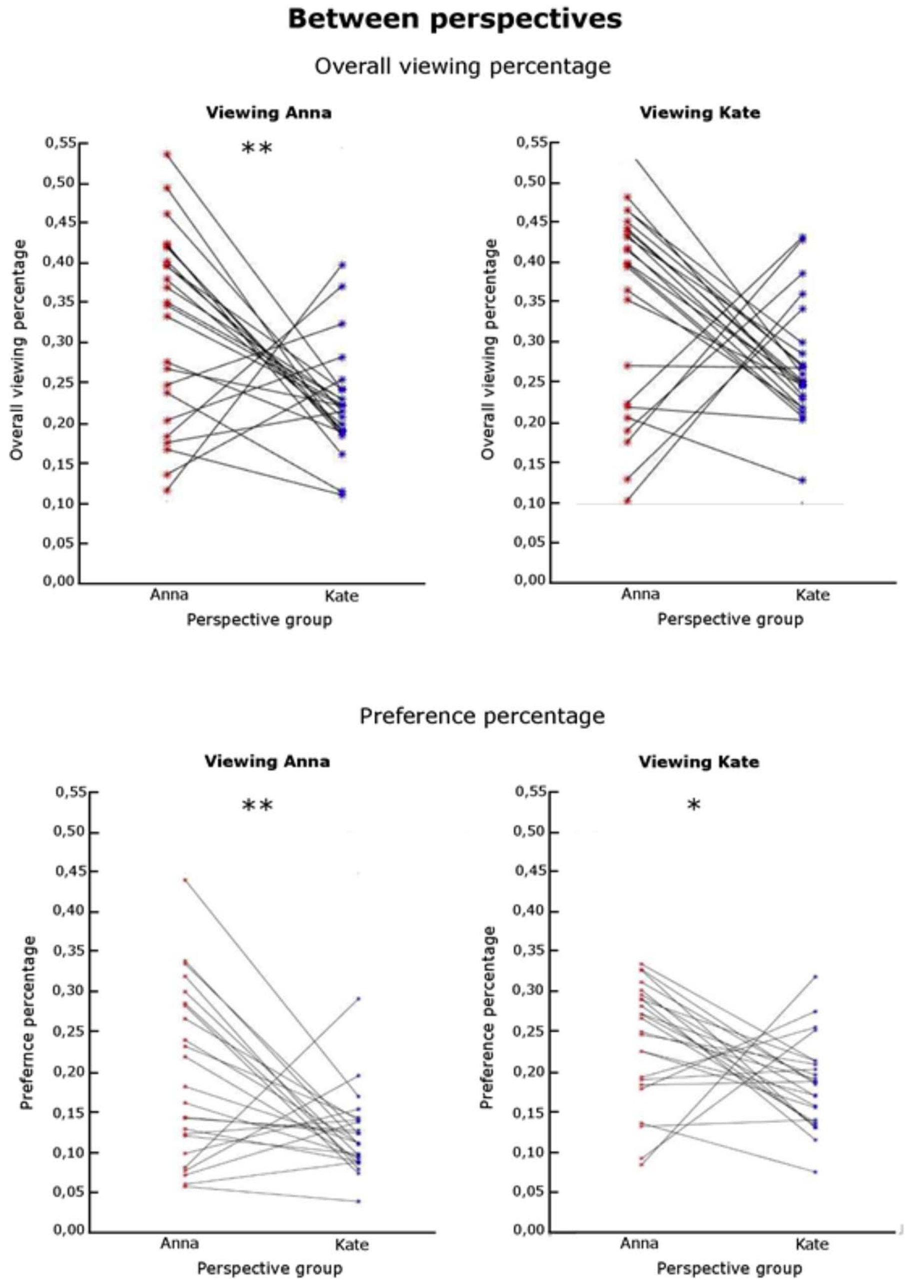

Fig. 5. Overall viewing (above) and preference (bottom) for the between perspective comparison. The overall viewing percentage is significantly higher for viewing the potential organ donor Anna when taking the perspective of Anna compared to taking the perspective of the potential organ recipient Kate in both overall viewing percentage and preference, as visible for most of the participants. A significance level of 0,05 is represented in the figure with an ∗, the significance level of 0,01 is depicted as ∗∗.

Emotional contagion rating. As a self-report measure, the subjects answered two emotional empathy questionnaires: Hatfield's Emotional Contagion Scale (Hatfield *et al.*, 1994) and the BIS/BAS scale (Carver and White, 1994). 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).

A conjunction analysis was performed to investigate if any of these scores as well as the size of the social network could drive the correlation of brain activity in the perspective task. The seven factors (Hatfield's Emotional Contagion Score, Hatfield's Emotional Contagion Scale, BIS scale, BAS drive, BAS fun seeking, BAS reward responsiveness as well as the social network size) were found to explain the ISC of brain activity in several brain areas, particularly in the occipital and parietal cortices. However, when comparedwith the brain areas significantly correlated with taking perspectives, no overlap between the scales and the brain activity could be found, suggesting that the areas for perspective-taking are not associated with the scores of emotional contagion.

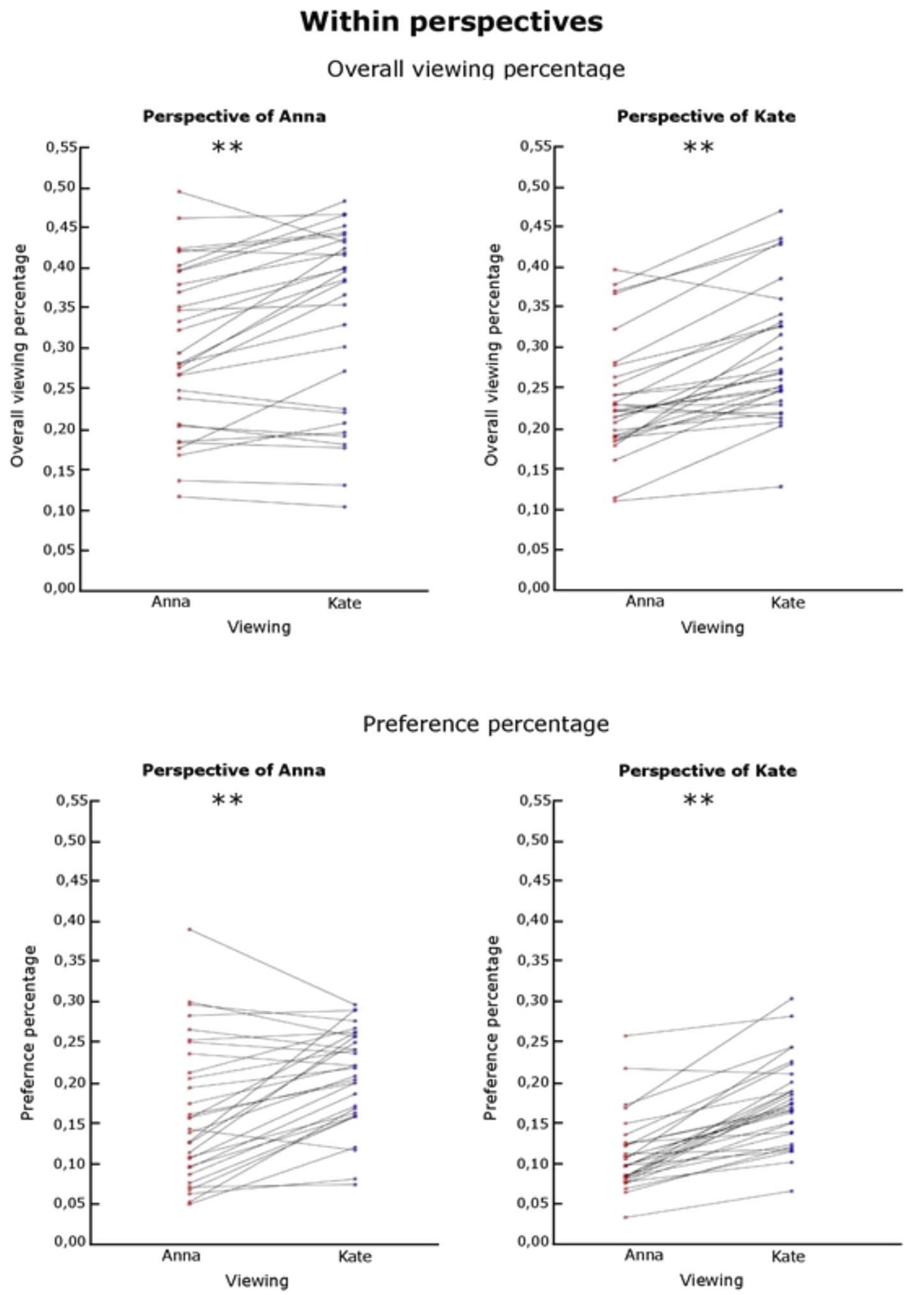

Fig. 6. Overall viewing (above) and preference (bottom) for the across perspective comparison. The overall viewing percentage is significantly higher for viewing the potential organ recipient Kate comparing participants in the same perspective (either of Anna or of Kate) for both overall viewing percentage and preference, as visible for most of the participants. A significance level of 0,05 is represented in the figure with an ∗, the significance level of 0,01 is depicted as ∗∗.

Discussion

We studied how taking a specific social perspective affects brain activity and eye movement patterns by measuring brain hemodynamic activity and eye movements during viewing of a movie clip from the perspectives of two different movie protagonists. Perspective-taking is an important skill of putting oneself into the shoes of someone else in order to understand the behaviour, feelings, mental states and actions of another human being. Here, the stimulus was chosen to be a feature film as it has been shown that ecologically valid, rich stimuli such as movies constitute a suitable vehicle to achieve the complexity of real life (e.g. Bartels and Zeki, 2004; Malinen *et al.*, 2007; Ylipaavalniemi *et al.*, 2009; Lahnakoski *et al.*, 2012). This is particularly important when using multidimensional social interactions to make them as credible and perceptible as possible as these stimuli tend to have ambiguous and convergent features that may be overlooked in isolated test settings. In this study, the ISC and eye tracking of 30 female subjects were compared when they took either the perspective of a potential organ donor Anna or the potential organ recipient Kate in a feature movie depicting organ donation. In addition, the subjects were asked to view the movie with either assuming the protagonists to be genetic sisters or to think that the younger sister was adopted as a newborn. When the participants watched the movie depicting the moral dilemma of refused organ donation between two sisters, significant differences in ISC of brain activity and eye movements were indeed observed between the taking of the perspective of the potential organ donor *vs* the potential organ recipient (Figure 2).

Inter-subject correlation in fMRI

In the following, we discuss possible differences in cognitive functions that were engaged based on the brain areas that showed significant ISC differences between the two perspective conditions; however, when doing this it is important to be cognizant of the potential caveats associated with reverse inference (Poldrack, 2011), although see also (Hutzler, 2014). Overall, there were higher number of occipital areas [e.g. fusiform gyrus (FUS), lateral occipital cortex (LOC) and ventral temporal cortex (VTC)] exhibiting stronger ISC during the perspective of the potential organ donor than when adopting the perspective of the potential organ recipient.

While the occipital areas are often associated with visual processing (which is most probably the case here, as the stimulus was a movie), the higher ISC when watching the movie from the perspective of the potential organ donor Anna in these areas could be equally based on processes linked to more basic visual processing and social perception (Loughead *et al.*, 2008, Trautmann *et al.*, 2009, Weisberg *et al.*, 2014,. Grosbras and Paus, 2006). Interestingly, one of the areas observed in this contrast, the cuneus, has been associated in previous studies with false belief and counterfactual reasoning in a social environment (Van Hoeck *et al.*, 2014).

Perhaps most interestingly, brain areas in the lateral frontal (DLPFC, IFG, middle frontal gyrus (MFG)) as well as medial frontal cortex (insula, PCC) temporal pole, precuneus and angular gyrus showed higher ISC in the potential organ donor condition (Figure 2). These areas have been previously associated with the neural processing of moral dilemmas (medial frontal cortex, PCC, insula, DLPFC) (Greene *et al.*, 2004; Robertson *et al.*, 2007; Harenski *et al.*, 2008), conflict monitoring (medial frontal cortex, IFG) (Goldin *et al.*, 2008; Solomon *et al.*, 2009; Egner, 2011; Dambacher *et al.*, 2014), self-reflection (medial frontal cortex, insula) (Modinos *et al.*, 2009, Hartwright *et al.*, 2015) as well as mentalising, empathy and perspective-taking (angular gyrus, medial frontal cortex, PCC, precuneus, temporal poles, insula, DLPFC, fusiform gyrus) (Lamm *et al.*, 2007, 2010, Lombardo *et al.*, 2010, Atique *et al.*, 2011, Schnell *et al.*, 2011, Sakaki *et al.*, 2012, Schmitgen *et al.*, 2016, Vistoli *et al.*, 2016).

In the reverse contrast, areas showing significantly higher ISC in the perspective of the potential organ recipient Kate were localised in the superior and medial temporal gyri and adjoining temporoparietal junction, regions which have been previously described as hubs for language processing (Homae *et al.*, 2003; Xu *et al.*, 2005; McNealy *et al.*, 2006; Kuperberg *et al.*, 2008; Zarate and Zatorre, 2008; Peeva *et al.*, 2010) gaze shift (Caruana *et al.*, 2014) as well as some aspects of social perspective-taking, theory of mind processes and empathy (Hynes *et al.*, 2006; Burnett and Blakemore, 2009; van der Meer *et al.*, 2011; Decety *et al.*, 2013; Kestemont *et al.*, 2013; Kestemont *et al.*, 2015; van Elk *et al.*, 2017). Furthermore, higher ISC in somatosensory areas during the potential organ recipient condition might also have reflected empathy towards the protagonist (Nummenmaa *et al.*, 2008).

The differences between ISC in the two perspectives probably arose from the differential roles of the characters in the movie and thus in the requirements for the perspective-taking. Although taking the perspective of both movie protagonists, the potential organ donor undergoing the moral dilemma as well as the potential organ recipient, suffering from terminal cancer, requires both cognitive and affective perspective-taking, the perspective of the potential organ donor is more cognitive in nature as e.g. pondering the different aspects and outcomes of the organ donation, whereas the potential organ donor concentrates more on affective aspects of perspective-taking as e.g. generating empathy for her suffering.

While the role of the potential organ donor Anna was one of an active agent who was able to (and had to) decide in a difficult moral dilemma, the role of the potential organ recipient Kate was rather passive, one of suffering and being in need for help, and target of empathy for the other characters in the movie as well as for the movie viewer. It has been shown that the moral responsibility is differently assigned to different agents: the more mature, active, autonomous, capable and aware an acting agent is judged to be, the more this person is held responsible for her/his (moral) actions and therefore requires more cognitive processing (Gray *et al.*, 2007). For example, a conscious adult is observed as more responsible than a child, and a child more than an animal. From this it can be inferred that taking the perspective of the potential organ donor required stronger engagement of moral processing and cognitive perspective-taking. Brain regions exhibiting significantly higher ISC when adopting this perspective (e.g. medial frontal cortex, IFG, DLPFC) have been shown to be associated with cognitive perspective-taking (Hynes *et al.*, 2006; Kalbe *et al.*, 2010; Sebastian *et al.*, 2012; Corradi-Dell'Acqua *et al.*, 2014) and thus support this suggestion.

On the other hand, taking the perspective of the passively suffering potential organ recipient might have required stronger empathetic resonance, which is again in line with the brain ISC findings observed in that perspective-taking condition in the present study. The effects of self-reported emotional contagion could not be determined on neither the ISC nor eye tracking results since there was very low between-subject variability in this measure.

Our two previous papers (Bacha-Trams *et al.*, 2017, 2018) report results obtained from the same dataset. However, the research question and thus the examined conditions are very different in each three studies. The first study (Bacha-Trams *et al.*, 2017) showed how the subject's brains were engaged when viewing the movie depicting the moral dilemma of the refusal of organ donation between the two sisters when the subjects were instructed to believe that the sisters were related either genetically or by adoption. We used ISC to study the differences in the brain activity caused by different instructions and found that brain areas previously associated with moral and emotional conflict regulation, decision-making and mentalising as the insula, cingulate, medial and lateral prefrontal, superior temporal and superior parietal cortices were found to be correlated when the subjects believed that the sisters were genetically related.

In the second study (Bacha-Trams *et al.*, 2018), we studied how thinking styles (analytic *vs* holistic) of the subjects influence their brain activity during viewing the film. We found that holistic *vs* analytical thinkers showed significant ISC in more extensive cortical areas than analytical thinkers, suggesting that they perceived the movie in a more similar fashion. Higher correlations in holistic thinkers were particularly found in occipital, prefrontal and temporal cortices. In analytical *vs* holistic thinkers, stronger co-ISC was observed in the right hemisphere fusiform gyrus, temporoparietal junction and frontal cortex.

Finally, in the present study, we analysed how adopting a social perspective of one of the actors was reflected in the brain activity of the participants. The role of the potential organ donor Anna requires an engagement of moral processing and cognitive perspective-taking, which is then reflected in higher ISC in e.g.

medial frontal cortex, IFG and DLPFC. The role of the potential organ recipient Kate is to passively wait for help and to be a target of empathy. This was reflected on brain areas of the brains' 'empathy network' (superior temporal, posterior frontal and anterior parietal areas).

Taken together, our three studies show that (i) background knowledge about the relationship between interacting persons in the movie, (ii) thinking styles of the participants and (iii) taking different social perspectives robustly modulate social cognition of the perceivers, and brain areas are flexibly recruited depending on the specific task in the same participants and with the same stimulus.

Eye tracking

The mean ISC for eye-gaze patterns (eISC) and eISC per perspective. The mean eISC analysis and the analyses per perspective revealed that the similarity of eye-gaze was higher in the perspective of the potential organ donor Anna and only the pairs when both subjects were in the perspective of Anna compared to the across perspective condition yielded in significantly higher correlations. These higher correlations might arise from the moral complexity of Anna's character: the potential organ donor Anna is in the position to decide to donate her organ or not; observing this character in order to process her dilemma could have helped the subjects in reflecting on the thoughts and feelings of this character and take her perspective.

The higher similarities of eye-gaze and ISC in the perspective of the potential organ donor Anna could also relate to the fact that some perspectives produce larger effects than others, as prior behavioural work on perspective-driven text and scene processing has shown, possibly due to task constraints or the number of factors relevant for a specific perspective (Anderson and Pichert, 1978; Kaakinen and Hyönä, 2008). In addition, participants may also interpret some perspectives with more overlapping prototypical knowledge (Kaakinen and Hyönä, 2008), which may increase the similarity of perception of the scenes and the associated brain activity and eye-gaze behaviour.

Further, the eISC analysis of the eye-gaze behaviour showed that the visual attention was more spread (measured by smaller similarity among the participants) when taking the perspective of the potential organ recipient Kate. This result could reflect the fact that the character of Kate receives help and support from all characters and may be a target of empathy of others, so that it may be more relevant to also observe other factors in the story such as the other family members instead of only focusing on the two protagonists.

Region of interest analysis: overall viewing percentage and viewing preference

Between perspectives. The analysis between perspective-taking conditions, i.e. contrasting the subjects viewing the movie from the perspective of Anna against the subjects watching the movie from the perspective of Kate, showed that subjects taking the perspective of Anna preferred to watch both movie characters Anna and Kate more than the subjects watching the movie from Kate's perspective. This finding might be explained by the larger moral complexity of Anna's character. As the character of Anna is in the situation to make the moral decision, following Anna's perspective requires the participants to actively gather information on the behaviour of both the potential organ donor Anna and the sick sister Kate as well as their mutual interaction. Observing and processing the character of Anna in detail might have helped the participants to put themselves in her position that required deciding in the morally heavy dilemma amidst reflecting on her thoughts and feelings. Observing and processing the character of Kate and the sisters' mutual interaction on the other hand may support to understand the moral considerations Anna is forced to do and weigh the effects that each decision would have on each one of the sisters.

Within perspectives. Comparing within perspective, i.e. when both participants either took the perspective of the potential organ donor Anna or the potential organ recipient Kate, showed that all participants, regardless of the perspective group they were in, preferred to watch the character of Kate. This finding could reflect the subjects having seen Kate as a target of empathy since observing facial expressions and body language of the target individual is essential to accurately identify feelings and feel them in oneself (Ekman and Friesen, 1967; Ekman, 1979; Bindemann *et al.*, 2008), viewing the potential organ recipient Kate could serve to induce empathic feelings and concern in the participants. Further, the potential organ recipient Kate gathers extensive visual attention (e.g. by directed gaze) from the other movie characters (family members). Thus, some of the interests in observing Kate could account for gaze cueing of the other characters' attention (Langton and Bruce, 1999). In particular, participants taking the potential organ donor Anna's perspective could be motivated to follow Anna's gaze cueing of visual attention in order to understand (and possibly simulate) the emotional consequences of the moral decision as part of the moral decision-making process of the character of Anna. As it has been shown that the eye-gaze could be guided into new interesting targets reinforcing the accumulation of socially relevant information by previously acquired information (Duchowski, 2007), cueing different targets as the two movie protagonists at the beginning of the movie could strengthen the differences between perspectives.

Physiological and behavioural measurements

The physiological measurements of heart and breathing rate showed no difference between the perspective groups as well as no specific correlation to either ISC or eye tracking, suggesting that the different conditions in which the movie was shown did not lead to different physiological reactions. The answers from the behavioural questionnaires suggest that the subjects were able to take the perspectives of the potential organ donor Anna and the potential organ recipient Kate similarly easy.

Given that in the present study only two social perspectives were compared in a complex social situation involving a difficult moral dilemma between two sisters, further studies with different movie scenarios (or even other materials such as auditory and written narratives) are needed to elucidate in further detail how specific brain areas are dynamically recruited across a larger variety of perspectives. Also, given that in this study the subjects were 30 healthy females, further studies should examine how male subjects would perceive the movie and in what extent the results would converge. The fact that the brain regions involved in perspective-taking differed between the two social perspectives in the present study provides evidence for the suggestion that ISC of brain activity represents similarity in high-level information processing as e.g. mental states across individuals rather than simply similarity in stimulus-driven neural activity (Hasson *et al.*, 2004; Nummenmaa *et al.*, 2012). Further, finding that the brain regions involved in taking perspectives of interior decorator and forensic detective in a previous study (Lahnakoski et al., 2014) recruited yet different brain regions suggest that perspective-taking highly dynamically recruits brain regions required in taking a given perspective, rather than there being some brain areas specific to perspective-taking. In conclusion then, it seems that the social setting, goals and relationships of the protagonists in the movie dynamically modulate a set of brain regions involved in adopting one *vs* the other social perspective as well as the eye-gaze behaviour.

Supplementary data

Supplementary data are available at *SCAN* online.

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Conflict of interest

None declared.

Contributions

M.B.T. planned thestudies, led and executed the experimental work, did the analysis and write the manuscript. E.R. assisted in analysing the data and commenting on the manuscript. E.G. developed methods, analysed the data and commented on the manuscript. M.S. and I.P.J. planned the studies, supervised the whole project and wrote the manuscript.

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