OXFORD

A drama movie activates brains of holistic and analytical thinkers differentially

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Abstract

People socialized in different cultures differ in their thinking styles. Eastern-culture people view objects more holistically by taking context into account, whereas Western-culture people view objects more analytically by focusing on them at the expense of context. Here we studied whether participants, who have different thinking styles but live within the same culture, exhibit differential brain activity when viewing a drama movie. A total of 26 Finnish participants, who were divided into holistic and analytical thinkers based on self-report questionnaire scores, watched a shortened drama movie during functional magnetic resonance imaging. We compared intersubject correlation (ISC) of brain hemodynamic activity of holistic *vs* analytical participants across the movie viewings. Holistic thinkers showed significant ISC in more extensive cortical areas than analytical thinkers, suggesting that they perceived the movie in a more similar fashion. Significantly higher ISC was observed in holistic thinkers in occipital, prefrontal and temporal cortices. In analytical thinkers, significant ISC was observed in right-hemisphere fusiform gyrus, temporoparietal junction and frontal cortex. Since these results were obtained in participants with similar cultural background, they are less prone to confounds by other possible cultural differences. Overall, our results show how brain activity in holistic *vs* analytical participants differs when viewing the same drama movie.

Key words: analytical–holistic thinking; neuroimaging; functional magnetic resonance imaging; intersubject correlation

Introduction

There are robust differences in thinking styles between people socialized in different cultures (Nisbett and Masuda, 2003; Nisbett and Miyamoto, 2005). A previous research has reported differences between holistically and analytically thinking indi-viduals in visual attention and object recognition (Baranski and Petrusic, 1999; Haun *et al.*, 2006; Winawer *et al.*, 2007; Tan *et al.*, 2008). Analytical thinkers tend to rely on object categorization based on rules and formal logic. They emphasize the meaning of single objects and attribute events to causes that are internal to the object or person they see. They further observe scenes

with narrowly focused visual attention and try to uncouple items from their contexts in which they are embedded, e.g. by attending to focal objects in visual scenes. In contrast, holistic thinking is characterized by thematic, context-dependent categorization of objects and by emphasis on relationships and similarities. Holistic individuals show broad focus in their visual attention and rely on contextual information when explaining social behavior (Nisbett and Masuda, 2003).

Individuals with different thinking styles also differ in their social orientations: analytical thinkers emphasize self-direction, autonomy, self-expression and independent social orientation, whereas holistic thinking is built on interdependent social orientation focusing on harmony, relatedness and connection. Individuals with an analytical thinking style view themselves as separate from social others in contrast to holistically thinking individuals who view themselves as interconnected to their social surroundings (Triandis, 1990; Markus and Kitayama, 1991). As a consequence, analytically thinking individuals define their happiness more often in socially disengaging emotion (e.g. pride) and can be motivated to symbolically enhance themselves at the expense of others, whereas holistically thinking individuals experience happiness as a socially engaging emotion (e.g. sense of closeness to others) and are less motivated by enhancement of themselves (Kitayama *et al.*, 2006a,b). Holistic and analytical modes of thinking are not mutually exclusive, however, as each individual has these styles to varying degrees (Foard and Kemler Nelson, 1984).

Movies are useful in studies of social perception as they depict interactions in real-life-like situations (Hasson *et al.*, 2004; Lahnakoski *et al.*, 2012). Advances in functional magnetic resonance imaging (fMRI) acquisition methods and data analysis algorithms (Bartels and Zeki, 2004; Hasson *et al.*, 2004) have made it possible to use naturalistic stimuli such as movies during fMRI. When viewing a film during brain scanning, both sensory cortices and 'higher-order' prefrontal and parietal cortical areas become synchronized across participants as captured by calculation of intersubject correlation (ISC; Jääskeläinen *et al.*, 2008; Hasson *et al.*, 2008).

Here, we examined differences in how participants with holistic *vs* analytical thinking styles process a shortened version of a drama movie [*My Sister's Keeper* (Curmudgeon Films, 2009), Nick Cassavetes (dir.)] during fMRI. The movie depicts a moral dilemma involving refusal of organ donation: the main character is a girl who fights for her right of physical integrity and self-determination as she decides to refuse to donate a kidney to her sister suffering from cancer. We used ISC to test for differences in blood oxygenation level-dependent fMRI signals between subjects with analytical and holistic thinking styles. Simultaneously, with fMRI, we also measured eye gaze patterns that have been previously observed to differ according to thinking style when viewing still pictures (Chua *et al.*, 2005).

One shortcoming in cross-cultural studies that are comparing the effects of analytical and holistic thinking styles on processing of naturalistic stimuli is that it is difficult to control the presence of other culture-specific variables that might covary with the analytical–holistic cognitive style. Due to this, we studied holistic and analytical participants within the Finnish culture as there is a spectrum of individuals with analytical to holistic cognitive styles within each culture (Martella and Maass, 2000; Kitayama *et al.*, 2006a; Knight and Nisbett, 2007; Henrich *et al.*, 2010; Talhelm *et al.*, 2014). We hypothesized that (i) there are differences in ISC between subjects with analytical and holistic cognitive styles with larger proportion of cortical areas showing higher ISC in holistic subjects given that subjects

with analytical thinking style might be more idiosyncratic in their perception and (ii) the eye gaze pattern will be more uniform/correlated in holistic thinkers than in analytical thinkers as it has been shown that analytical thinkers fixate more on distinct focal objects (Chua *et al.*, 2005). Given the differences in viewing behavior of naturalistic still scenes, we further hypothesized that differences will be found in visual brain areas in the occipital cortex as well as areas involved in object recognition, motion perception and eye gaze in the parietal lobule and temporal cortex. In addition, we hypothesized that as the movie depicts organ donation, integrity of the body and the right for self-determination in a family context, brain areas related to processing of social interactions, mentalizing and self-reflection show differential ISC in analytically *vs* holistically thinking participants. Such areas include default mode network (Bernhard and Singer, 2012) structures, the ventromedial prefrontal cortex (VMPFC) and the temporoparietal junction (TPJ) as well as brain areas associated with emotional processing, such as the amygdala and dorsolateral prefrontal cortex (DLPFC).

Material and methods

Participants

We studied 33 healthy female participants (age range: 19–39 years; mean age: 26 years; one left-handed participant; laterality index of right-handed participants: 84.5%). None of them reported any history of neurological or psychiatric disorders. All participants had either normal or corrected-to-normal vision. Seven participants had to be excluded from the analysis: three due to discomfort in the scanner, one as she did not fill the behavioral questionnaire and three as their native language was Russian. Thus, the final number of participants was 26. They were all Finnish citizens raised in Finland with Finnish as their native language. The classification into holistic and analytical thinking participants was done according to answers in a questionnaire (see below).

All participants declared to be sufficiently proficient in English to follow the movie without subtitles. The study was carried out in accordance with the Declaration of Helsinki (World Medical Association, 2013), and all participants provided informed consent as a part of the protocol approved by the ethics committee of Aalto University.

Stimuli and Procedure. The feature film, *My Sister's Keeper* (Curmudgeon Films, 2009), Nick Cassavetes (dir.), edited down to 23 min and 44 s yet retaining the main storyline, was shown to the participants during fMRI. This movie tells the story of two sisters named Anna and Kate, with Anna undergoing a moral dilemma. In the course of the movie, Anna is asked to donate her kidney to Kate, who is fatally ill from cancer. Anna refuses the organ donation and Kate dies. The participants watched the same movie four times in two separate scanning sessions on two different days. On separate viewings, the subjects were either made to believe that the sisters were related genetically or that the younger sister Anna had been adopted as a newborn. Further, the participants were asked to take either the perspective of the potential donor (Anna) or the perspective of the potential recipient (Kate), once in the condition of genetic and once in the condition of non-genetic sisters (Figure 1). The order of the different viewing conditions was counterbalanced between the participants. Results related to manipulation of a priori information (Bacha-Trams *et al.*, 2017) and perspective-taking are reported
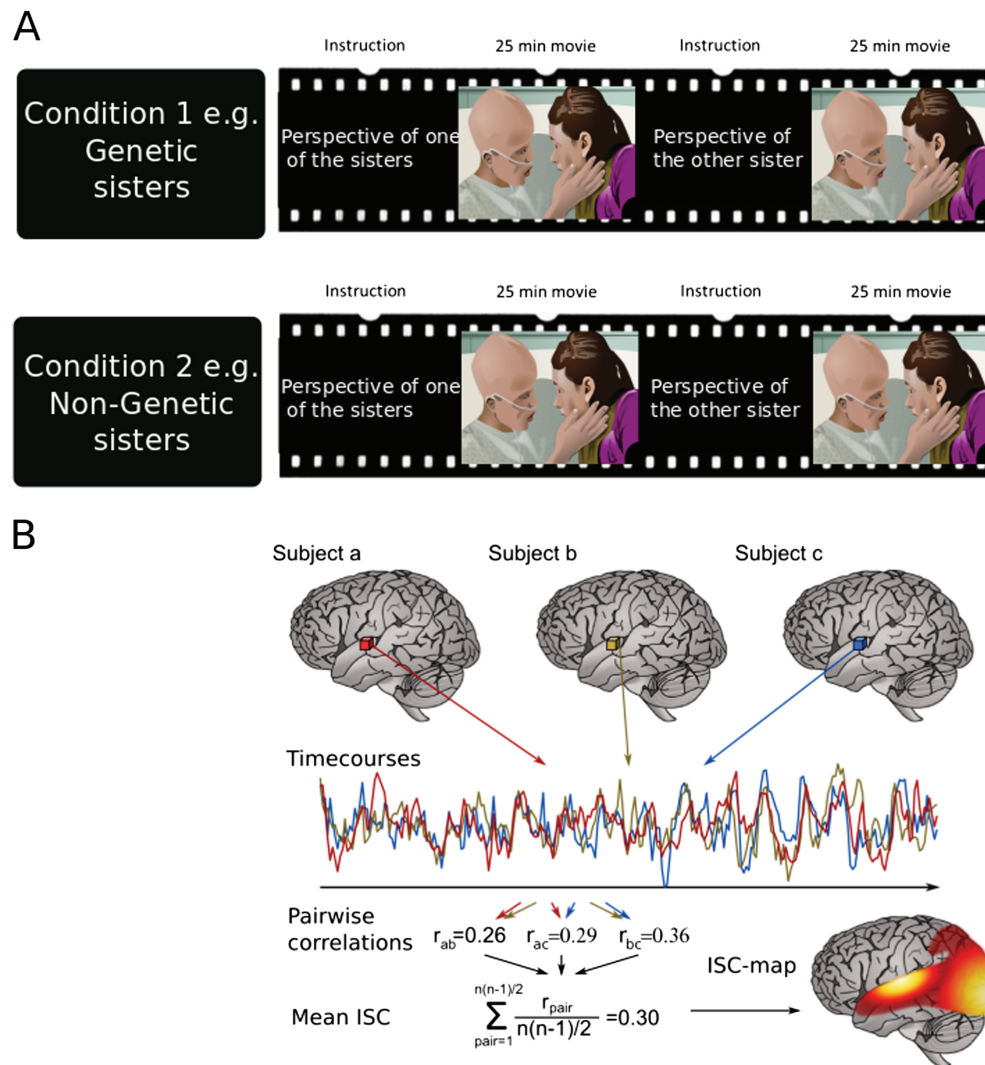
Fig. 1. Experimental procedure and ISC analysis in the movie-viewing task (figure taken from Bacha-Trams *et al.*, 2017). (A) Participants viewed the same movie stimulus 4 times, in a 2 × 2 design, assuming that the movie characters are either genetically related or not as well as in the perspective 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 ISC, pair-wise correlations across participants were calculated between the time series of each voxel from all the fMRI recordings. Please note, that the ISC map in this figure shows exemplary data to illustrate the method.

elsewhere and not included here. All four viewings of a subject were combined in the first main analysis with subjects split into analytical and holistic thinkers based on the median analytical-holistic-score (AHS) questionnaire score (Figure 2). In addition, separate analyses were performed to contrast the following: (i) the ISC between the subjects with highest analytical and highest holistic scores in the AHS questionnaire and (ii) the ISC between different perspectives within the same thinking style subjects to test whether differences in analytical *vs* holistic subjects ISC are consistent across the perspective-taking tasks.

fMRI acquisition

Prior to the beginning of the experiment, scanning procedures were explained and the participants were asked to avoid bodily movements during the scans. The movie was shown to the participant with the Presentation software (Neurobehavioral Systems Inc., Albany, CA), which synchronizes the onset of the stimuli with the beginning of the functional scans. The

participants were able to watch the movie in a viewing distance of 33–35 cm on a semitransparent screen back projected from a data projector (PT-DZ8700/DZ110X Series; Panasonic, Osaka, Japan) via a mirror located above their eyes. The audio track of the movie, adjusted individually to be loud enough to be heard over the scanner noise, was played to the participants with a Sensimetrics S14 audio system (Sensimetrics Corporation, Malden, MA). To acquire the brain-imaging data, a 3T Siemens Magnetom Skyra (Siemens Healthcare, Erlangen, Germany) scanner was used, which is located at the Advanced Magnetic Imaging Centre, Aalto University, and equipped with a standard 20-channel receiving head–neck coil. Anatomical images were acquired using a contrast between gray and white matter (T1-weighted) MP-RAGE pulse sequence (repetition time (TR) = 2530 ms; echo time (TE) = 3.3 ms; TI = 1100 ms; flip angle, 7 degrees; 256 × 256 matrix; sagittal slices, 176; resolution, 1 mm^3). A total of 712 whole-brain echo-planar imaging (EPI) volumes were acquired with T2*-weighted EPI sequence sensitive to the Blood-oxygen-level-dependent
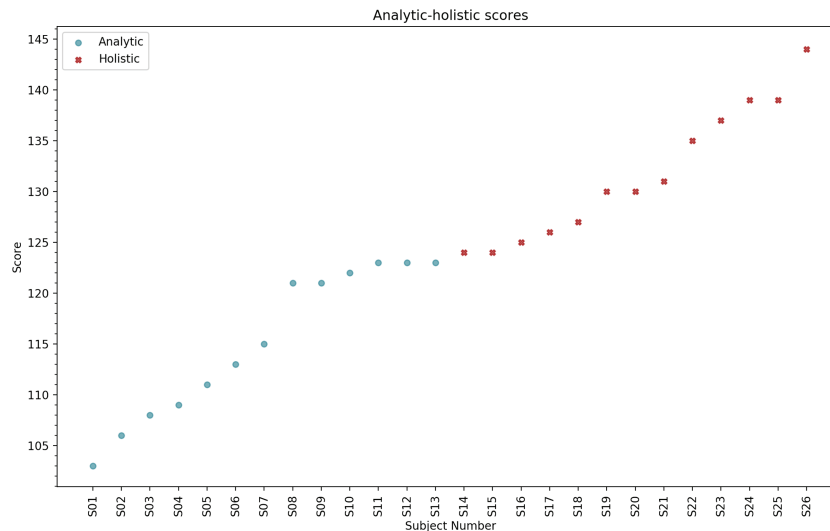
Fig. 2. Scores and classification into analytical and holistic participants. After viewing the movie all participants were asked to answer a 24-item questionnaire (Choi *et al.*, 2007) to assess their thinking style on a bipolar analytical–holistic dimension. Participants were divided into 2 groups with a cut-off at the median score of 123 across all participants, resulting in groups of 13 holistic and 13 analytical participants, respectively.

(BOLD) contrast (TR = 2000 ms; TE = 30 ms; flip angle, 90 degrees; 64 × 64 matrix; axial slices, 35; slice thickness, 4 mm; in-plane resolution, 3 × 3 mm). In addition, heart and respiration rates were recorded during fMRI with the Biopac system. Instantaneous values of heart rate and breathing rate were estimated with DRIFTER software package (Särkkä *et al.*, 2012).

Recording of eye movements

During fMRI scans, eye movements were recorded from all participants using the EyeLink 1000 eye tracker (SR Research Ltd, Mississauga, Ontario, Canada; sampling rate = 1000 Hz, spatial accuracy better than 0.5°, with a 0.01° resolution in the pupil-tracking mode). From the 29 participants the data of 3 participants had to be excluded from the final data analysis due to technical problems (with the rejection criteria of blinks to be at maximum 10% of the duration of the scan and a majority of blinks and saccades being <1 s in duration) resulting in 26 subjects for the eye tracking analysis. Before starting the eye-movement recording, the eye tracker was calibrated once with a nine-point calibration. Saccades were detected with a velocity threshold of 30 degrees/s and an acceleration threshold of 4000 degrees/s². Due to the length of the experiment, which did not comprise intermediate drift correction, mean effect of the drift was corrected retrospectively. First, the mean of all fixation locations was calculated over the entire experiment for each participant, and then the fixation distributions were rigidly shifted so that the mean fixation location coincided with the grand mean fixation location over all participants.

Classification of the participants into the analytical and holistic group

Behavioral questionnaire. After viewing the movie all participants were asked to answer a 24-item questionnaire (Choi *et al.*, 2007) to assess their thinking style as either holistic or analytical. Participants were divided into 2 groups with a cut-off at the median score of 123 across all participants (13 holistic and 13 analytical participants, respectively; Figure 2).

As an additional self-report measure, the participants' disposition for catching emotions from others was assessed with two emotional empathy questionnaires: Hatfield's Emotional Contagion Scale (Hatfield *et al.*, 1994) and the behavioral inhibition system/behavioral activation system (BIS/BAS) scale (Carver and White, 1994; Supplementary Table S1).

fMRI pre-processing

Standard fMRI pre-processing was performed using FMRIB (Oxford Centre for Functional MRI of the Brain) Software Library (FSL) (www.fmrib.ox.ac.uk) and custom MATLAB code (available at https://version.aalto.fi/gitlab/BML/bramila/). Head motion was corrected in EPI images using MCFLIRT, and then the images were coregistered to the Montreal Neurological Institute's 152 2 mm template in a two-step registration procedure using FLIRT. In the first step the EPIs were coregistered to participant's anatomical image after brain extraction (9 degrees of freedom), and in the second step the coregistration started from anatomical to standard template (12 degrees of freedom). Further, to remove scanner drift, 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 were applied. In order to clean the BOLD time series to avoid motion and physiological artifacts, 24 motion-related regressors were used to control for signal from deep white matter, ventricles and cerebral spinal fluid locations (Power *et al.*, 2014). Cerebrospinal fluid mask was obtained from SPM8 (file csf.nii); white matter and ventricle masks were obtained from Harvard–Oxford atlas included with FSL.

Eye-movement analysis

Participant-wise gaze fixation distributions were compared across the participants with analytical and holistic cognitive styles. Individual heat maps were generated by modeling each fixation as a Gaussian function using a Gaussian kernel with an s.d. of 1 degree of visual angle and a radius of 3 s.d.s. The heat maps were generated in time windows of 2 s corresponding to the TR used in the fMRI. Spatial similarities between each pair of heat maps across the eye-tracking sessions were calculated using Pearson's product-moment correlation coefficient (ISC of
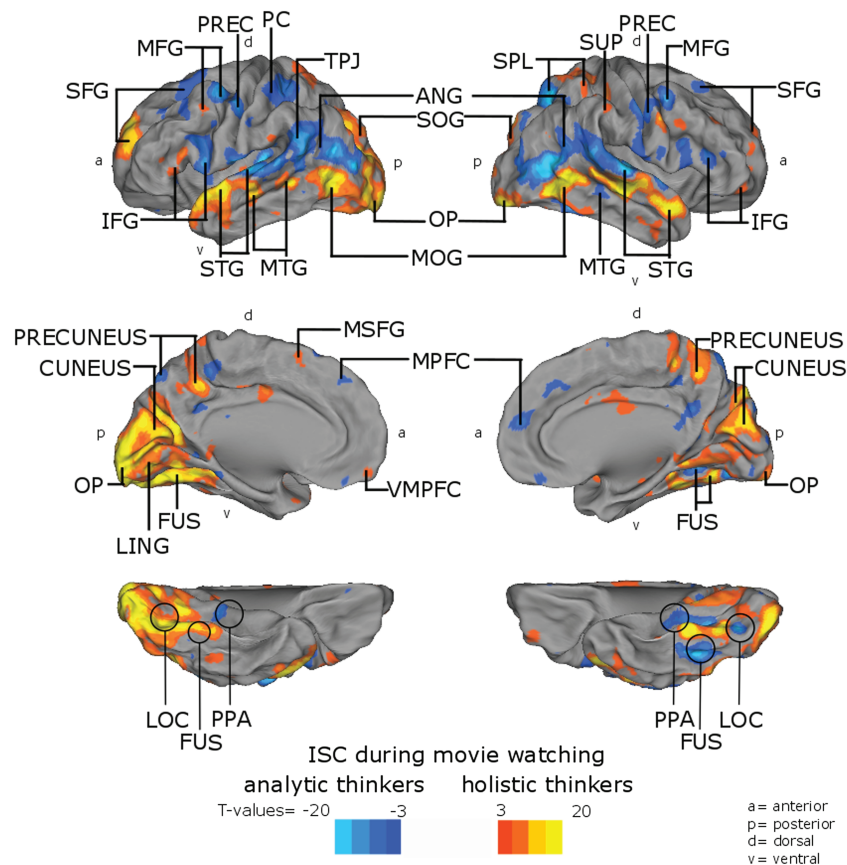
Fig. 3. Contrast between ISC of brain activity in the holistic *vs* analytical thinkers during watching of the movie (*n* = 26; lateral, medial and ventral view from top to bottom). Cold colors indicate higher ISC in analytical thinkers; warm colors indicate higher ISC in holistic thinkers. See text for details. MFG, middle frontal gyrus; MOG, middle occipital gyrus; MTG, middle temporal gyrus; MSFG, medial superior frontal gyrus; PC, postcentral gyrus; SUP, supramarginal gyrus; TP, temporal pole.

eye gaze, eISC; Nummenmaa *et al.*, 2014). A similarity matrix was obtained with correlations between each pair for each of the 712 time windows.

First, the mean eISC scores over all 712 time windows were examined. These mean scores were acquired by 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 of the group differences was analyzed by contrasting pairs in which both participants were classified as analytical with pairs in which both were classified as holistic. Permutation-based *t*-test with 100 000 permutations were used to avoid making assumptions about the data distribution. In this procedure the data were mixed randomly to change groupings and differences in the resulting new randomized groups were used to form an estimated distribution of the data. A comparison of how many of the permuted random partitions into groups build a more extreme group mean difference than the one observed with the original grouping yielded the final *P*-values.

Second, in order to further study overall differences between gaze styles, we analyzed the spread of gazes. For this, we counted the number of pixels that surpassed a given percentage threshold of maxima of the heat maps. A lower threshold leads to fewer pixels (and vice versa). Median pixels counts over time windows were then compared between the holistic and analytical participants using permutation-based *t*-test (100 000 permutations). This was repeated for multiple thresholds between 10% and 90%.

Third, the temporal patterns in the eye gaze differences between the two cognitive styles were examined by analyzing the fixation distribution differences time window by time window. In each of the 712 time windows we contrasted the pairs of 2 analytical participants with pairs of 2 holistic participants and assessed the statistical significance of the difference with a permutation-based *t*-test that performs 100 000 permutations of the data. Benjamini–Hochberg false discovery rate (BH-FDR) with $q < 0.05$ was used to correct the *P*-values of the 712 time windows for multiple comparisons. Finally, also the mean saccade amplitudes and fixation durations were compared across analytical and holistic participants. We calculated the means of fixation duration and saccade amplitude over the whole course of the movie for each viewing. A permutation-based *t*-test with 100 000 permutations was performed to compare the scores between analytical and holistic participants.

ISC analysis of brain activity during movie

To examine the similarity of brain activity across participants with different cognitive styles, we performed ISC using the ISC toolbox (Kauppi *et al.*, 2014). For each voxel the toolbox computes a similarity matrix between participant pairs and within same participant for all four repetitions of viewings with the conditions being the following: (i) shared assumption that the sisters in the movie are genetically related; (ii) shared assumption that the younger sister was adopted; (iii) shared perspective of the to-be-donor sister; and (iv) shared perspective of the

Table 1. ISC clusters for the analytical and holistic thinkers

Holistic > analytical

Cluster name	Cluster size	Coordinates			t-value
Occipital	34535	48	−52	2	−35.39
IFG	1261	−16	50	28	−21.12
ACC	930	−6	−12	36	−10.20
Frontal pole	725	22	66	−6	−7.47
PREC	359	36	−4	40	−12.03
PREC	220	−50	4	48	−10.95
TPJ	218	−46	−36	28	−8.81
PREC	210	58	2	40	−20.88
Putamen	207	12	4	0	−5.92
Frontal pole	197	34	46	−6	−6.78
Frontal pole	190	−26	62	−14	−7.82
VMPFC	150	−8	48	−12	−6.47
Amygdala	149	−16	−4	−18	−8.35

Analytical > Holistic

Cluster name	Cluster size	Coordinates			t-value
ANG/STG	8683	48	−68	12	35.23
TPJ	7101	−48	−36	14	30.77
SPL	1073	−28	−40	54	11.80
PREC	896	−38	−2	52	16.59
Precuneus	597	10	−46	44	10.12
Cerebellum	382	−4	−76	−40	11.47
TP	307	−52	4	−32	8.91
Cerebellum	266	32	−64	−60	16.76
VMPFC	244	2	38	−16	5.92
ANG	212	−24	−60	38	15.47
Cerebellum	164	−34	−62	−54	8.30
LING	154	−18	−72	−4	11.10
LING	146	−20	−42	−12	12.24
TP	139	50	4	−38	7.05
OC	133	−36	26	0	8.88
Frontal pole	125	−30	62	0	6.27

Abbreviations: ACC, anterior cingulate cortex; MFG, middle frontal gyrus; OC, orbitofrontal cortex; TP, temporal pole.

to-be-recipient sister. The resulting similarity matrix was therefore of size 104 × 104 (4 conditions × 26 participants). Each value of the correlation matrix is a result of the correlation between the BOLD time series of the pair of participants considered for the selected voxel.

First, the ISC matrices were analyzed using representational similarity analysis (RSA) approach (Kriegeskorte *et al.,* 2008), where we compared the neural ISC separately against two behavioral models—eISC and score distances. For the scores, we created a model matrix (104 × 104) whose elements were negated absolute distances between the scores of all pairs of subjects (0 for the same subject under 4 conditions). Using the two models, we computed Spearman's rank correlation with the upper triangular parts of ISC matrices. Statistical significance of the correlations was assessed with a permutation-based-t-test that performs 10 000 row and column-wise randomization of the model matrices (Mantel test, see Glerean *et al.,* 2016).

Second, the overall ISC differences between participants with analytical and holistic cognitive styles were examined by contrasting, for each voxel, the ISC scores of pairs in which both participants were classified as analytical with pairs in which both participants were classified as holistic. In order to control for the gaze differences between groups, we first removed eISC from voxel ISC's via linear regression and the residual ISC's were used in the following group difference analysis. The statistical significance of the differences was assessed by first trans-

forming the correlation values into z-scores with the Fisher's Z-transform and then computing t-values and corresponding P-values using a permutation-based approach (Glerean *et al.,* 2016). The results were corrected for multiple comparisons using BH-FDR with $q < 0.05$. For visualization purposes, all results were also cluster corrected by removing any significant clusters smaller than 4 × 4 × 4 voxels. Summary tables thresholded according to the P-value were generated. Unthresholded statistical parametric maps can be found in NeuroVault (https://neurovault.org/images/65891).

Results

Participants were classified into an analytical and a holistic thinking group based on self-reporting questionnaire. The questionnaire is based on a bipolar scale, with participants scoring below the median of 123 points defined as analytical and participants above 123 points as holistic. Figure 2 shows the questionnaire scores for each of the study participants ($n = 26$: 13 analytical and 13 holistic participants).

We observed a larger extent of the cortex showing significant ISC, as well as significantly more similar eye gaze patterns, among the holistic than analytical participants. The precuneus, cuneus and anterior superior parietal lobule (SPL) and the supramarginal gyrus on the right lateral side exhibited higher ISC
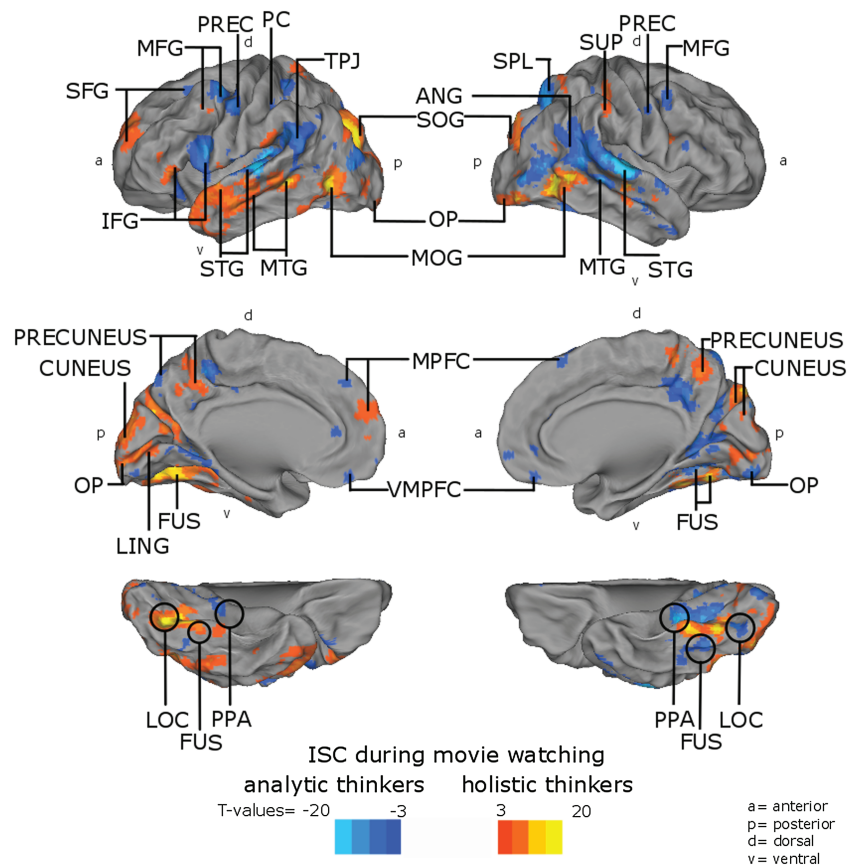
Fig. 4. Contrast of ISC of brain activity between the highest-scoring analytical and highest-scoring holistic thinkers on the bipolar scale during watching of the movie ($n = 12$; lateral, medial and ventral view from top to bottom). Cold colors indicate higher ISC in analytical thinkers; warm colors indicate higher ISC in holistic thinkers. MFG, middle frontal gyrus; MOG, middle occipital gyrus; MTG, middle temporal gyrus; PC, postcentral gyrus; SUP, supramarginal gyrus; TP, temporal pole.

in holistic participants (Figure 3; Table 1). In the temporal lobe, areas in the middle and anterior superior temporal gyrus (STG) and posterior middle temporal gyrus also exhibited higher ISC in the holistic thinkers. The largest cluster of significantly higher ISC in holistic *vs* analytical thinkers was localized in extensive areas of the medial and lateral occipital cortex, particularly in the left hemisphere. This cluster comprises the occipital pole (OP) and the lateral occipital gyrus in both hemispheres as well as the left calcarine, lingual gyrus (LING) and fusiform gyrus (FUS; Figure 3).

Further areas of higher ISC in holistic participants were localized in the anterior superior and inferior frontal gyri (IFG) as well as medially in the VMPFC and middle superior frontal gyrus (SFG). In the reverse contrast, higher ISC for analytical thinkers was observed in the occipital angular gyrus (ANG) of both hemispheres and right FUS. Areas of higher ISC were also found in the TPJ, right SPL and the posterior parts of the STG in both hemispheres. Several clusters of higher ISC were further found in the precentral cortex (PREC), the SFG, IFG and middle frontal gyrus and medial prefrontal cortex (MPFC) in both hemispheres.

In addition, Figure 4 shows differences in ISC of brain activity when comparing the highest-scoring analytical and highest-scoring holistic thinking individuals ($n = 12$: 6 individuals with the highest analytical *vs* 6 individuals with the highest holistic scores). Despite the much smaller sample size, this contrast replicated the findings of the broader comparison across the whole group of participants shown in Figure 3.

We also compared the subjects with analytical and holistic thinking styles when they took the perspective of the movie protagonist Anna (Supplementary Figure S1) and when they took the perspective of the movie protagonist Kate (Supplementary Figure S2). The findings across these two contrasts were highly similar, thus indicating that differences in ISC between analytical and holistic thinkers did not depend on the particular perspective that was adopted. Probably due to the smaller number of observations, some areas observed in the main contrast shown in Figure 3 failed to survive thresholding, and many areas were seen less robustly in these perspective-specific contrasts than in the main contrast that combined the perspectives.

We also compared highly analytical participants *vs* low analytical participants (Supplementary Figure 3) and highly holistic participants *vs* low holistic participants (Supplementary Figure 4). These contrasts showed similar results as in the main contrast (analytical *vs* holistic thinkers); however, the results are partly more difficult to interpret, probably as a combination of being a weaker contrast with those scoring at the middle of scale ('low analytical/low holistic') having a mix of analytical and holistic tendencies, and at the same time the analysis suffering from much reduced N.

The mean eye gaze patterns were more similar in holistic than analytical participants ($n = 26$; permutation-based *t*-test, $P = 0.0292$). Figure 5 shows the eye gaze patterns for the holistic group (red) and the analytical group (blue) over the time course of the movie presentation. Time windows with
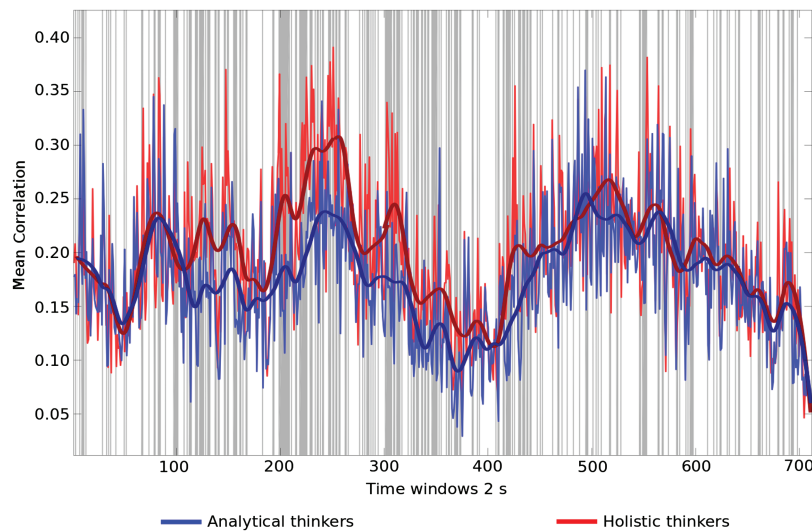
Fig. 5. Eye tracking for the time course of the movie ($n = 26$; 1830 pair-wise comparisons; 712 time windows of 2 s). The mean correlations of the eye gaze patterns are shown in blue for the analytical thinking participants and in red for the holistic thinkers. The time windows shown in grey indicate significant differences between the correlated eye gaze patterns of both group, with a majority of time windows showing higher correlations in holistic thinkers.

a length of 2 s in which the difference between both groups was significant (permutation-based *t*-test for each time window individually; *P*-value threshold, $P < 0.025$; two-tailed test, confidence level $= 0.05$) are indicated in gray. A total of 36% of all time windows showed significantly different eye gaze patterns between groups; 84% of these correlations were higher in holistic *vs* analytical thinkers. Furthermore, we found that gaze areas over 2 s windows were typically larger for holistic thinkers. The difference in median gaze areas was significant for binarization thresholds between 50% and 60% (*t*-test followed by permutations, *t*-value $= -1.7543$, $P = 0.0420$; two-tailed, threshold $= 55$%).

Similarities in BOLD activity were correlated with similarities in eye movements in various cortical regions, particularly in occipital, parietal and temporal lobes, as depicted in Supplementary Figure 5. As eISC model used in this analysis was removed from BOLD ISCs, this finding did not explain the group differences depicted in Figure 3. Furthermore, various regions in Figure 3 were also found sensitive to the fine-scale (Euclidean) differences in individual analytical–holistic scores. This is depicted in Supplementary Figure 6 showing voxels that were found significant in RSA between BOLD ISCs and score distances.

The breathing rate was more similar in holistic than in analytical participants (*t*-test followed by permutations, *t*-value $= -3.47$, $P = 5.22 \times 10^{-4}$). However, for both heart rate (*t*-test followed by permutations, *t*-value $= 0.95$, $P = 0.35$), and valence arousal measurements (Mantel test with 100 000 permutations; valence, $P = 0.18$; arousal, $P = 0.052$) we did not detect significant differences between analytical and holistic thinkers. Similarly, the self-ratings of emotional contagion did not differ between analytical *vs* holistic thinking style subjects (emotional contagion score: *t*-value $= -0.1437$, $P = 1$; scale: *t*-value $= -0.4863$, $P = 1$; BIS/BAS: BIS *t*-value $= -1.9420$, $P = 0.4059$; BAS Drive: *t*-value $= 1.2250$, $P = 1$; BAS-Fun-seeking: *t*-value $= 0.6260$, $P = 1$; BAS Reward Responsiveness: *t*-value $= -0.8895$, $P = 1$ all tests with Bonferroni corrections; Bonferroni correction was used instead of FDR since the number of comparisons was lower than in case neuroimaging data where the high number of voxels results in Bonferroni being too conservative).

Discussion

Culture shapes how we perceive reality, ranging from perception of time as cyclic *vs* linear, perception of objects in relation to their backgrounds *vs* objects *per se* in pictures to appreciating the world as continuums *vs* in categories (Nisbett and Masuda, 2003; Nisbett and Miyamoto, 2005). Such differences have been attributed to the individual's position on a continuum between holistic *vs* analytical cognitive styles (Varnum *et al.*, 2008). Here, we found different ISC of brain activity for analytical and holistic thinkers in several areas across the whole brain.

Importantly, unlike in previous studies, we did not study analytical *vs* holistic thinkers from different cultures but participants of the same (Finnish) culture, who were classified to be either holistic or analytical thinkers based on answers they gave in a questionnaire. By studying individuals from the same cultural background, we could better control for a multitude of factors, which might confound results when comparing participants from different cultures. Societal differences could be caused by the length of time that the societies have been industrialized and degree to which political institutions have a tradition of being democratic. In addition, there are substantial differences in the genetic and linguistic background of participants from different cultures. Different languages and other forms of communication could for example shape the participants' perception and evaluation of a situation or the stimulus that is shown to them (Whorf, 1956; Heider and Olivier, 1972; Davidoff *et al.*, 1999; Madden *et al.*, 2000; Winawer *et al.*, 2007; Thierry *et al.*, 2009).

Because of this broad set of cultural differences, there are many possible factors that might account for thinking differences that have been observed between East and West. In our study, the participants who all live in the Finnish society are much more homogenous. All our 26 participants were Finnish citizens who were raised in Finland with Finnish as their native language. Their age range is 19–39 years. Naturally, it is possible, despite the rather uniform cultural background of Finnish speaking Finns in Finland, that the subjects might have had variability in their cultural background not captured by our measures; however, any such variabilities are most likely less than

if we had compared holistic subjects from an Eastern culture with analytical subjects from a Western culture. Further, we did not contrast analytical and holistic tasks but provided the participants with the same stimuli and tasks.

We observed a larger extent of the cortex showing stronger ISC, both in a contrast over all participants and when comparing the highest-scoring analytical and holistic thinking individuals, as well as significantly larger eye-movement ISC among the holistic than analytical participants (Figures 3–5). Even though a number of cortical regions exhibited higher ISC in the analytical participants, the significantly larger extent of brain areas showing higher ISC in holistic thinkers suggests that the holistic participants performed the task more similarly. Further, similarity in results across the two perspective-taking conditions suggests that the observed ISC differences between the subjects with analytical and holistic subjects were stable across at least these two tasks (Supplementary Figures 1 and 2).

It has been previously shown that when faced with a stimulus depicting several objects, analytical thinkers focus on separate objects, which are different for different participants (Nisbett and Miyamoto, 2005). In contrast, holistic participants focus more on contextual information and relationships between items or people, thus keeping a wider focus of attention, observing the overall picture rather than single objects. In accordance, one might assume that the analytical participants, focusing more on specific details, adopted more across-participants divergent viewing approaches, while the holistic participants focused their perception on the wider aspect of social relatedness and connections, resulting in higher brain and eye-movement ISC and larger gaze areas in holistic than analytical thinkers.

Traditionally, the left hemisphere has been identified to be more involved in processing analytical and verbal information, and the right hemisphere processing holistic, context-sensitive and spatial information (Jackson, 1878; Ornstein, 1972; Moscovitch, 1979; Springer and Deutsch, 1989; Reuter-Lorenz and Miller, 1998). Although associating hemispheres with thinking styles has been questioned (e.g. Gur *et al.*, 1992), this connection has been applied to differences between analytical and holistic processing in different cultures: holistic individuals from Eastern cultures emphasized right-hemisphere functions in comparison to analytical individuals of Euro-American cultures (Rozin *et al.*, 2016).

In our study, however, we report contrasting findings: For the analytical thinkers we found higher ISC in occiptial areas [fusiform face area (FFA) parahippocampal place area (PPA) and lateral occipital compex (LOC)] of the right hemisphere, whereas the ISC was higher in the left hemisphere for the holistic thinkers. Naturally, these discrepancies between studies might have been due to differences in measures, as we used the ISC measure in the present study that provides a voxel-wise estimate of where in the brain activity across the movie viewings was more similar within one *vs* the other group of subjects, even though a good general correspondence between ISC and more traditional Generalized linear model (GLM)-based analyses has been reported in a previous methodological study (Pajula *et al.*, 2012).

Previous studies have also found differences between holistic and analytical thinkers sampled from different cultures in a part of the 'what' processing stream in the ventral visual occipital cortex, which is involved in the identification and recognition of visual stimuli (Mishkin *et al.*, 1983). Specifically, Goh *et al.* (2010) reported differences in brain activity for analytical and holistic participants in the FFA, PPA and LOC, with analytical participants

showing more selective response for faces in the FFA and holistic participants showing more selectivity to houses compared to faces in the lingual areas. Furthermore, hemispheric asymmetry has been observed in these areas: more selectivity for faces was discovered in the left FFA in analytical thinkers and in the right FFA in holistic participants. No differences between analytical and holistic participants were found in the PPA (Goh *et al.*, 2010).

Thus, out of the regions that have been associated with both object processing and analytical thinking, only the ones in the right hemisphere showed stronger ISC in our analytical participants. The homologous areas in the left hemisphere showed higher ISC in the holistic participants. Similarly, for regions associated in previous studies with background processing (e.g. Goh *et al.*, 2004), higher ISC was found in the right hemisphere for analytical *vs* holistic thinkers. Thus, paralleling previous reports, we found differential ISC of brain hemodynamic activity in the ventral occipital areas—FFA, PPA and LOC—for analytical and holistic participants, but in contrast to previous studies (Goh *et al.*, 2004; Goh and Park, 2009) the differences in ISC were (strongly) right-lateralized for analytical thinkers and left-lateralized for holistic thinkers. Naturally, our experimental setup was different in that we measured ISC during naturalistic viewing of a movie wherein most scenes showed the bodies and faces of the movie protagonists often in close-up shots, whereas previous studies have contrasted strength of hemodynamic activations to pictures of faces *vs* houses between analytical and holistic subjects. However, functional differences have been reported between left and right fusiform gyri that might help explain our findings. For example, it has been shown that the right FUS is superior compared to left in discriminating between individual faces with the role of the left FUS apparently more limited to recognition of familiar faces (Levy *et al.*, 1972; de Moraes *et al.*, 2014) Tentatively, then, the tendency of analytical subjects to pay closer attention to objects, including faces, might have resulted in more consistent recruitment of the right FUS than in case of holistic subjects.

Importantly, unlike in previous studies, we did not contrast analytical and holistic tasks but provided the participants (grouped into analytical and holistic thinkers) with the same stimulus and task (i.e. movie watching with specific instructions). Perhaps, most importantly, the stimulus in our study was a drama movie with a story line developing over time and containing social interactions amidst staging a moral dilemma. In the previous studies, participants have been presented with still pictures of scenes with objects and background.

Further, areas in the VMPFC, DLPFC and dorsomedial prefrontal cortex were found to be significantly more correlated between holistic than analytical participants. Keeping in mind the caveats associated with reverse inference (Poldrack, 2011), although one can speculate on differences in cognitive functions engaged between holistic and analytical thinkers during movie viewing based on the brain areas that showed differences (Hutzler, 2014). Higher ISC in the VMPFC in the holistic participants could have reflected holistic thinkers' higher similarity in perceiving the moral conflict of refusing organ donation, involving the integrity of one's body and the right for self-determination, as the VMPFC has been associated with moral processing and self-reflection in previous studies (Moll *et al.*, 2003; Harenski *et al.*, 2008; Decety and Wheatley, 2015). Further, higher ISC was observed in subjects with holistic thinking style in the OP, which has been observed to be specifically activated by pursuit eye movements in humans (Petit and Haxby, 1999).

Notably, analytical thinkers specifically showed higher correlation in areas associated with visual and object processing.

Various brain areas that were more highly correlated among analytical thinking participants, such as the SPL, ANG, TPJ, postcentral gyrus, PREC, STG and precuneus, were found to be involved in object processing (Takahama *et al*., 2010), observation of (biological) motion (Vaina *et al*., 2001; Dinstein *et al*., 2008), processing of eye movements (Brown *et al*., 2006; Trenner et al., 2008) and social gaze shift (Ohlendorf *et al*., 2007; George and Conty, 2008; Itier and Batty, 2009; Caruana *et al*., 2014). Further, areas in the ANG and TPJ were activated specifically in analytical thinkers, in light of previous studies possibly reflecting intentional (ANG) and emotional (TPJ) mentalizing (Atique *et al*., 2011; Fehr *et al*., 2014). Thus, taken together, specific areas in the prefrontal cortex and OP associated with moral processing, self-reflection and control of eye movements were highly correlated in holistic thinkers. In contrast, other areas predominantly in the parietal and temporal cortices, associated with object and motion processing as well as intentional and emotional mentalizing, showed higher ISC among the analytical thinkers. It may thus be tentatively concluded that the holistic thinkers followed more the ongoing moral dilemma, whereas the analytical thinkers focused more on details such as specific objects and gazes between the movie characters. When interpreting potential functions of specific brain areas in this study one should, however, keep in mind that the task of the participants to assume perspective of a given protagonist, along with providing on different runs differential a priori information about the movie protagonists, might have affected the perceptual strategies of the participants compared to free movie viewing, where the viewers are 'guided' by the movie director. This should be tested in future studies. Further, as this study was performed solely in one (the Finnish) culture, it remains open if similar results would be found in a different culture or across cultures. A cross-cultural study should be performed in future to address the question if it is rather the thinking style or the actual culture that has a greater role in the present findings.

In conclusion, we found overall larger extent of cortex showing stronger ISC in holistic *vs* analytical participants with shared cultural background when they were watching a movie depicting a social moral dilemma. This, together with more similar eye gaze patterns in holistic participants, suggests that analytical participants focus on smaller details during movie viewing and are thus more idiosyncratic in their perceptual strategies of perceiving the movie. Overall, our results point out that there were robust differences in how analytical and holistic participants processed the movie.

Author's contribution

M.B.T. is responsible for planning the studies, leading and executing the experimental work, doing the analysis and writing the manuscript. Y.A. contributed in planning the studies, analyzing data and commenting on the manuscript. E.B., E.G., E.R., J.K. and M.K. assisted in analyzing the data and commenting on the manuscript. M.S. and I.P.J. helped in supervising the whole project and writing the manuscript.

Acknowledgements

Supplementary data

Funding

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