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NEURAL CORRELATES OF GROUP BIAS DURING NATURAL VIEWING

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ABSTRACT

Individuals from different social groups interpret the world in different ways. This study explores the neural basis of these group differences using a paradigm that simulates natural viewing conditions. Our aim was to determine if group differences could be found in sensory regions involved in the perception of the world or were evident in higher-level regions that are important for the interpretation of sensory information. We measured brain responses from two groups of football supporters, while they watched a video of matches between their teams. The time-course of response was then compared between individuals supporting the same (within-group) or the different (between-group) team. We found high inter-subject correlations in low-level and high-level regions of the visual brain. However, these regions of the brain did not show any group differences. Regions that showed higher correlations for individuals from the same group were found in a network of frontal and subcortical brain regions. The interplay between these regions suggests a range of cognitive processes from motor control to social cognition and reward are important in the establishment of social groups. These results suggest that group differences are primarily reflected in regions involved in the evaluation and interpretation of the sensory input.

INTRODUCTION

Our perception of the world is influenced by the presence of others (Allport, 1954; Asch, 1955; Cialdini & Goldstein, 2004; Milgram, 1974). We are particularly influenced by membership of social groups, which play a significant role in guiding our interpretation of events and our opinions of others (Sherif, Harvey, White, Hood, & Sherif, 1961; Amodio, 2014; Xiao, Coppin, & Van Bavel, 2016). The value humans place on social groups is illustrated by the ease and rapidity with which humans form groups and the psychological benefits gained by being a member of a group (Tajfel, 1982; Turner, Hogg, Oakes, Reicher, & Wetherell, 1987). A challenge to understanding group bias is revealing the specific cognitive and neural processes that give rise to differences in behaviour. A key question in this regard is whether group differences in neural processing occur at early stages of processing when sensory information is encoded or whether they are evident at later stages of processing, which are more involved in interpreting the input (Molenberghs, 2013; Cikara and Van Bavel, 2014).

Evidence for group differences in neural response at early stages of processing is shown by the response to own-race and other-race faces in regions of visual cortex, such as the fusiform gyrus (Golby, Gabrieli, Chiao, & Eberhardt, 2001; Lieberman, Hariri, Jarcho, Eisenberger, & Bookheimer, 2005). In these studies, there is a higher response to own-race faces, which is interpreted as showing a bias to perceive individuals from the in-group. A complementary pattern of results is evident in the amygdala, which responds more to other-race faces (Cunningham et al., 2004; Hart et al., 2000). These differences correlate with implicit measures of in-group bias and have led researchers to interpret this as evidence of negativity toward out-group members (Phelps et al., 2000; Wheeler & Fiske, 2005). Interestingly, these group effects in the fusiform gyrus and the amygdala are evident with

minimal group paradigms and can be influenced by both task and context (Van Bavel et al., 2008; 2011; Freeman et al., 2010; Amodio et al., 2014). Further evidence for a neural correlate of group differences at early stages of processing is evident in regions involved in the perception of action in response to the actions of in-group and out-group members (Molenberghs, Halasz, Mattingley, Vanman, & Cunnington, 2013).

It remains unclear, however, whether group differences in behaviour are more associated with the way information is interpreted (Molenberghs, 2013). For example, Cikara and colleagues found that positive in-group outcomes for baseball fans (success of the favoured team or failure of the rival team) were correlated with activity in the ventral striatum (Cikara, Botvinick, & Fiske, 2011). Other regions associated with the evaluation of social value such as the insula, cingulate gyrus, the temporal-parietal junction (TPJ) and medial prefrontal cortex have also been shown to discriminate between in-group and out-group members (Cheon et al., 2011; Hein, Silani, Preuschhoff, Batson, & Singer, 2010; Mathur, Harada, Lipke, & Chiao, 2010; Freeman et al., 2010; Xu et al., 2009; Cheon et al., 2011; Richeson et al., 2003). The flexibility of these regions is demonstrated by similar in-group bias when the groups are defined by the minimal group paradigm (Morrison, Decety, & Molenberghs, 2012; Van Bavel, Packer, & Cunningham, 2008; Volz, Kessler, & von Cramon, 2009).

Although these previous studies have provided important insights into the neural basis of group differences, the world seen in the controlled experimental setting used in many neuroimaging experiments bears a limited resemblance to our experience in real life, which is typically more complex and dynamic. To overcome this limitation, Hasson and colleagues (Hasson, Nir, Levy, Fuhrmann, & Malach, 2004) developed a novel neuroimaging approach in which natural viewing conditions are simulated by presenting participants with movies. The

data is analysed by comparing the time-courses of response in corresponding regions across subjects. This approach has been used to show that there are significant inter-subject correlations or similarities in the neural response, particularly in sensory regions of the occipital and temporal lobe (Hasson et al., 2004; Hasson, Malach & Heeger, 2010).

Here, we use the inter-subject correlation paradigm to explore differences in the neural response for individuals from different social groups. Our study was motivated by a classic paper by Hastorf and Cantril (1954), who asked Princeton and Dartmouth students to describe what happened in a contentious football match played between their teams. The majority of Princeton students blamed Dartmouth players for the rough play, whereas the Dartmouth students argued that the number of infractions was the same for both teams. The marked differences in the reports from the different student groups led them to conclude that they had seen a different game. In our study, we compared the time-course of response from individuals who were supporters of different football teams, while they watched a movie of matches between the two sides. Our hypothesis was that brain regions that showed larger within-group compared to between-group inter-subject correlations are associated with the cognitive processes evident in group bias.

METHODS

Participants

18 male participants (mean age: 20.9) took part in this study. All participants were neurologically healthy, right-handed, and had normal or corrected-to-normal vision. 9 participants were supporters of Chelsea Football Club and 9 participants were supporters of Manchester United Football Club. Similar numbers of participants have been used in previous studies using an inter-subject correlation paradigm (Hasson et al., 2004; 2008ab). To ensure that strong group biases were evident, we recruited participants who had on average supported their team for over 15 years (mean \pm SEM: 15.2 + 1.2) and had attended over 25 games (mean \pm SEM: 25.6 + 14.0). Written consent was obtained for all participants and the study was approved by the York Neuroimaging Centre Ethics Committee.

Stimulus

A movie was constructed by taking audio-visual segments from matches between Chelsea (<https://www.chelseafc.com/>) and Manchester United (<http://www.manutd.com/>). There were a total of 33 segments. Each segment showed a significant moment (e.g. a goal, missed penalty, receiving a trophy) and was designed to convey either a positive or negative reaction among the supporters of the rival teams. The mean duration of each clip was 23 seconds (range: 9 – 39 sec). There were a similar number of positive clips for both teams. The movie was back-projected onto a custom in-bore acrylic screen at a distance of approximately 57 cm from the participant with all images subtending approximately 15° of visual angle.

fMRI acquisition

All scanning was conducted at the York Neuroimaging Centre (YNiC) using a GE 3 Tesla HDx Excite MRI scanner. A Magnex head-dedicated gradient insert coil was used in conjunction

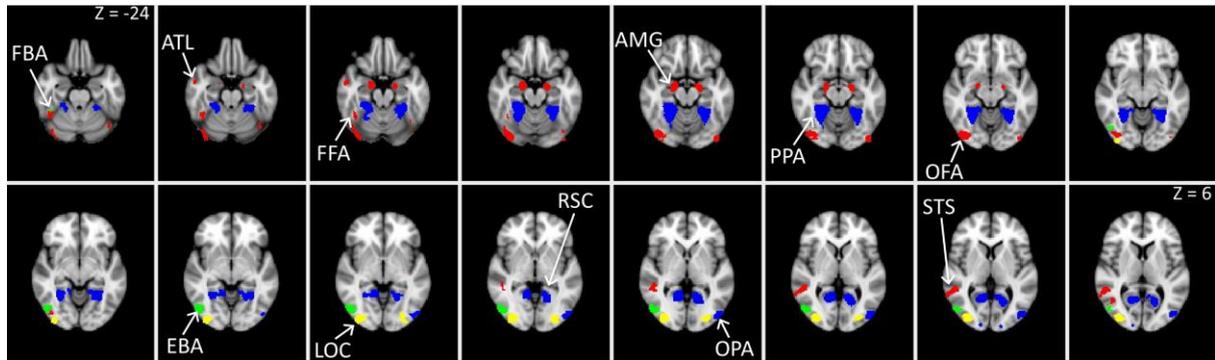
with a birdcage, radiofrequency coil tuned to 127.7MHz. Data were collected from 38 contiguous axial slices via a gradient-echo EPI sequence (TR = 3s, TE = 32.5 ms, FOV = 288 x 288 mm, matrix size = 128x128, voxel dimensions = 2.25 x 2.25 mm, slice thickness = 3 mm, flip angle = 90°). T1-weighted in-plane FLAIR images were acquired (TR = 2.5 s, TE = 9.98 ms, FOV = 288 x 288 mm, matrix size = 512 x 512, voxel dimensions = 0.56 x 0.56 mm, slice thickness = 3 mm, flip angle = 90). Finally, high-resolution T1-weighted structural images were acquired (TR = 7.96 ms, TE = 3.05 ms, FOV = 290 x 290 mm, matrix size = 256 x 256, voxel dimensions = 1.13 x 1.13 mm, slice thickness = 1 mm, flip angle = 20).

The fMRI data was analysed with FEAT v5.98 (<http://www.fmrib.ox.ac.uk/fsl>). In all scans the initial 9s of data were removed to reduce the effects of magnetic stimulation. Motion correction (MCFLIRT, FSL) was applied followed by temporal high-pass filtering (Gaussian-weighted least-squared straight line fittings, sigma=50s). Spatial smoothing (Gaussian) was applied at 6mm FWHM. Functional data were first registered to a high-resolution T1-anatomical image and then onto the standard MNI brain (ICBM152).

fMRI Analysis

To analyse the data from the experimental scan, the time-course of response from each voxel was converted from units of image intensity to percentage signal change. We measured regions of interest using three different methods. First, we compared responses in early visual areas using the probabilistic masks based on visual field maps developed by Wang and colleagues (Wang et al., 2015). The maps used included V1, V2, V3, V4, LO1, LO2, PHC1, PHC2, V3a, V3b, LO1, LO2, MT and MST. Next, we compared responses in high-level, category-selective regions of visual cortex. These regions were defined by a localizer scan that involved 5 stimulus conditions: faces, bodies, inanimate objects, places and scrambled images (see

Davies-Thompson et al., 2012). Images from each condition were presented in a blocked-design. 10 images (each image was presented for 700 msec with a 200 msec ISI) were presented in each block and a 9 s grey fixation screen was presented between blocks. Each condition was presented 4 times in a pseudo-randomized order. Boxcar models of each stimulus block were convolved with a gamma haemodynamic response function to generate regressors for each condition. Face-, place-, object- and body-selective regions were defined using the contrast of the response to each condition compared to each of the other conditions. For example, face-selective contrasts included: face>place, face>object, face>body, face>scrambled. Individual participant data were then entered into a higher-level group analysis using a mixed-effects design (FLAME, <http://www.fmrib.ox.ac.uk/>). Regions of interest were then created by averaging the statistical maps for each condition separately and then thresholding at $Z > 2.3$ (S Figure 1). This generated face-selective (fusiform face area: FFA, occipital face area: OFA, superior temporal sulcus: STS, anterior temporal lobe: ATL, amygdala: AMG), place-selective (parahippocampal place area: PPA, retrosplenial cortex: RSC, occipital place area: OPA), object-selective (lateral occipital complex: LOC) and body-selective (extrastriate body area: EBA, fusiform body area: FBA) masks (Malach et al., 1995; Kanwisher et al., 1997; Epstein & Kanwisher, 1998; Downing et al., 2001). Finally, we performed a whole brain analysis using the 55 anatomical regions (48 cortical and 7 sub-cortical) defined by the Harvard Oxford Atlas. The probabilistic atlas was thresholded to generate masks in which each voxel was assigned to the region with the highest probability.



S Figure 1 Category-selective regions of interest from the localizer scan. Face-selective regions (fusiform face area: FFA, occipital face area: OFA, superior temporal sulcus: STS, anterior temporal lobe: ATL, amygdala: AMG) are shown in red. Place-selective regions (parahippocampal place area: PPA, retrosplenial cortex: RSC, occipital place area: OPA) are shown in blue. Object-selective (lateral occipital complex: LOC) regions are shown in yellow. Body-selective (extrastriate body area: EBA, fusiform body area: FBA) regions are shown in green.

Voxels within each region were averaged to give a single time series for each ROI in each participant. Figure 1 shows the way that the data were analysed to determine relative differences in the neural response of participants from the same group or from different groups. For each region, the time-course of response for each participant was correlated (Pearson r) with participants from their own supporter group (r_w – within-group correlations) or with participants of the other group (r_b – between-group correlations). A Fisher's z -transform was applied to the correlations, prior to further statistical analysis. A repeated-measures ANOVA with Region and Group (within, between) was then used to analyse the data. Post-hoc t -tests were then used to determine which regions showed significantly higher within-group compared to between-group correlations.

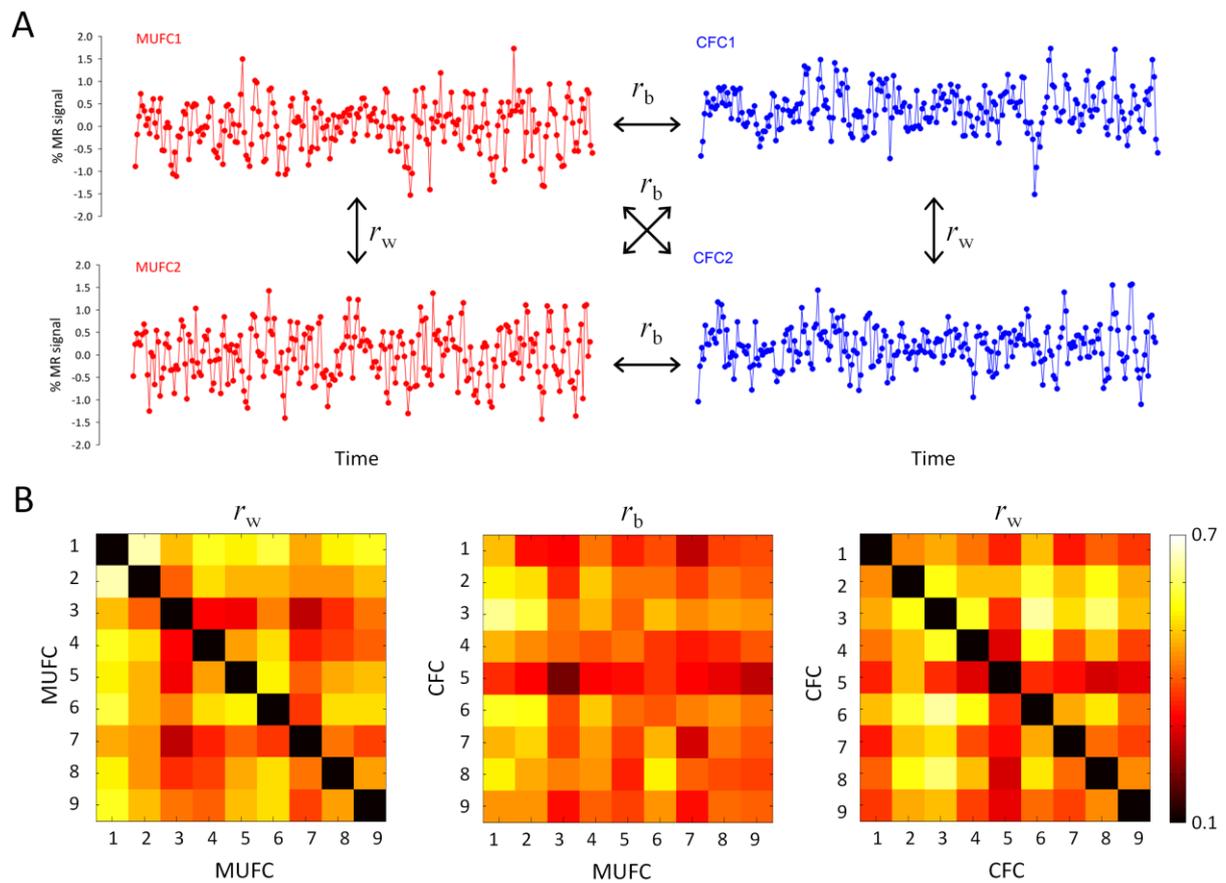


Figure 1 Within-group and between-group inter-subject correlations (ISC) from one brain region. (A) ISC were measured by taking the time-course of neural response from one individual and correlating this with the corresponding time-course from a different individual from the same group (within-group, r_w) or with an individual from a different group (between-group, r_b). Individuals were supporters of Chelsea Football Club (CFC) or Manchester United Football Club (MUFC). (B) Within-group and between-group correlations were calculated for each combination of individuals. This process was repeated for all regions.

Finally, we performed an orthogonal analysis by comparing the spatial pattern of response at each time-point for participants from the same (within) or different (between) groups. At each time point, the signal from each of the 55 regions from the Harvard-Oxford masks was measured for each participant. This vector of 55 numbers was then correlated

with the corresponding vector from a different participant who was either from the same group or from a different group. This generated a t-value for each time-point that reflected the difference between the within-group spatial pattern and the between-group spatial pattern. The group difference in the spatial pattern was calculated for each group separately. This allowed us to determine how within-group and between-group differences in the spatial pattern of response varied over time.

RESULTS

Visual field regions

First, we compared within-group and between-group correlations in the time-courses from the visual field regions (Fig. 2A). Despite the free viewing and complex nature of the movie, we found significant inter-subject correlations (ISC). The magnitude of the ISC varied across regions (Region: $F(13, 221) = 96.0, p < 0.0001$). The highest correlations were evident in early visual regions: V1 (0.57 ± 0.01) and V2 (0.46 ± 0.01). However, there was no difference between the within-group and between-group correlations (Group: $F(1, 17) = 0.001, p = 0.97$, Region * Group: $F(13, 221) = 0.57, p = 0.87$).

To determine the connectivity between regions, we compared the time-series of responses within participants (Fig. 2B). There was significant variation in the magnitude of the intra-subject correlations between regions (range: 0.11 – 0.92) suggesting distinct differences in processing. To determine how the regions were inter-connected a hierarchical clustering analysis was performed (<https://www.mathworks.com>) using an unweighted average distance method for computing the distance between clusters and $1 - \text{correlation}$ value as the distance metric (Fig. 2C). This shows distinct groups that correspond to early visual (V1-V3), ventral-occipital (V4, VO1-2, PHC1-2) and lateral-occipital regions (V3a, V3b, LO1-2, MT, MST). Taken together, these results show that, despite marked differences in the time-courses of response between these visual field regions revealed by the intra-subject correlations, there were no significant group differences in the inter-subject correlations.

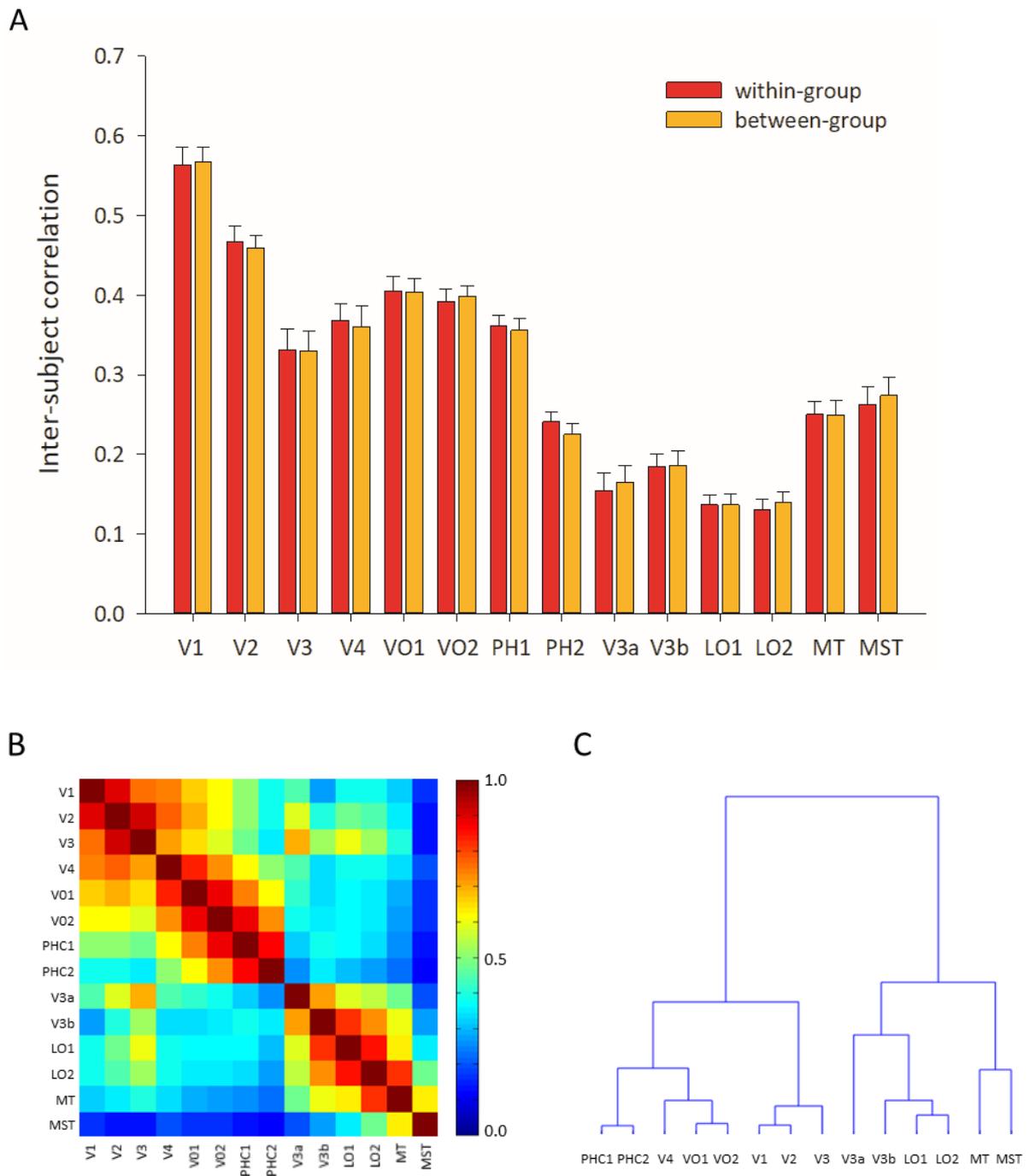


Figure 2 (A) Within-group and between group inter-subject correlations in visual field regions. There was no effect of group in any region. (B) Intra-subject correlations in the time-courses of response across all visual field regions. (C) Hierarchical clustering of the data revealed groups of regions that correspond to early visual, ventral-occipital and lateral occipital regions.

Category-selective regions

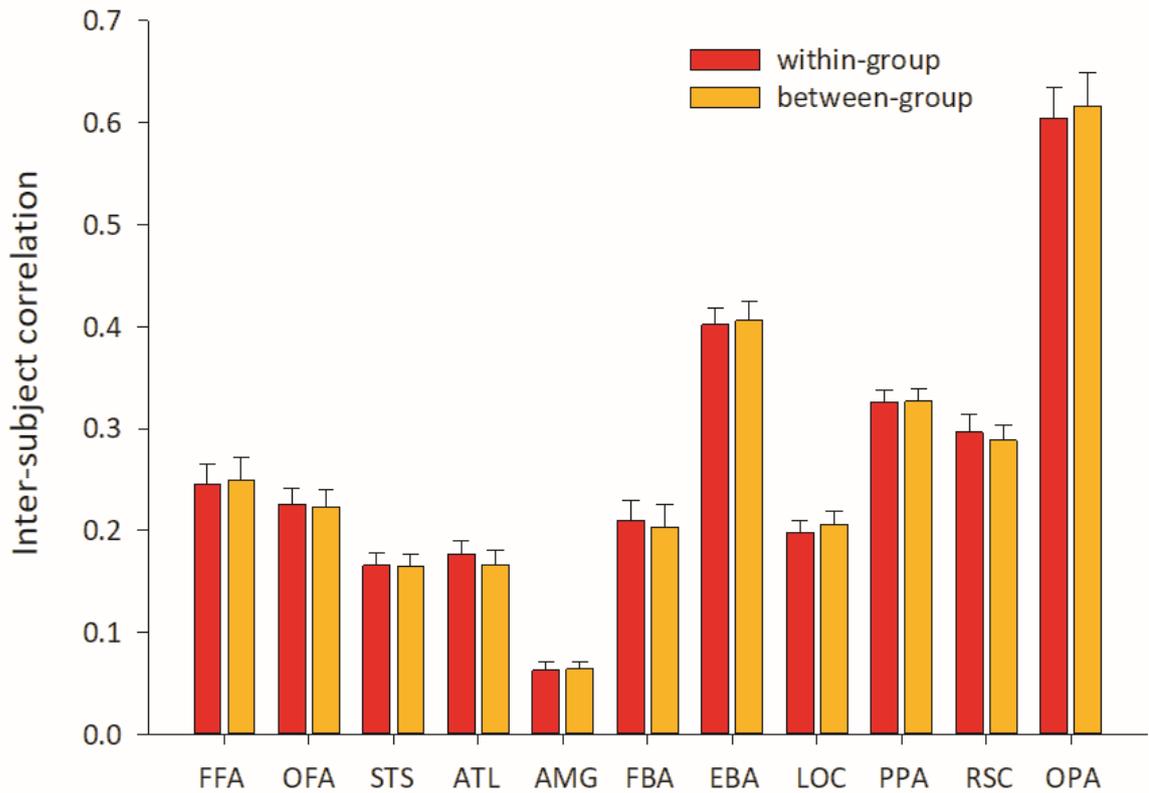
Next, we compared ISCs in the category-selective regions (Fig. 3A). The magnitude of the ISC varied across regions (Region: $F(10, 170) = 108, p < 0.0001$). The highest correlations were evident in the place-selective OPA (0.61 ± 0.02) and body-selective EBA (0.40 ± 0.01), perhaps reflecting the dominance of these object categories in the movie. However, again there was no difference between the within-group and between-group correlations (Group: $F(1, 17) = 0.0001, p = 0.99$, Region * Group: $F(10, 170) = 0.53, p = 0.87$).

To determine the connectivity between regions, we compared the time-series of response within participants (Fig. 3B). There was significant variation in the magnitude of the intra-subject correlations between regions (range: 0.18 – 0.76) suggesting distinct differences in processing. To determine how the regions were inter-connected a hierarchical clustering analysis was performed on the correlation matrix (Fig. 3C). This shows the relative similarity in the time-course of response across regions. There were similar neural responses among the face-selective (FFA, OFA) or the place-selective (PPA, RSC) regions. These intra-subject correlations show that category-selective networks have distinct time-courses of response. Nevertheless, the inter-subject correlations show that there were no group differences.

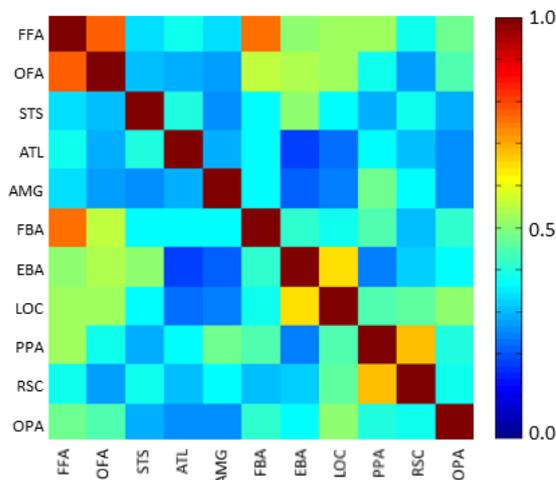
It is interesting to note that all the inter-regional correlations in the visual field and category-selective regions were positive. It is conceivable that significant negative correlations may have emerged, particularly between higher visual areas that are selective for different aspects of the visual scene. For example, the FFA responds more to faces than places, whereas the PPA responds more to places than faces. There are two possible reasons why we might not have found negative correlations. The first is that category-selective regions such as the FFA and PPA also respond positively to images from non-preferred object

categories (Ishai et al., 1999, Andrews, 2005, Ewbank et al., 2005). The second is that, in contrast to conventional neuroimaging paradigms, changes during a movie are likely to affect many properties of the image.

A



B



C

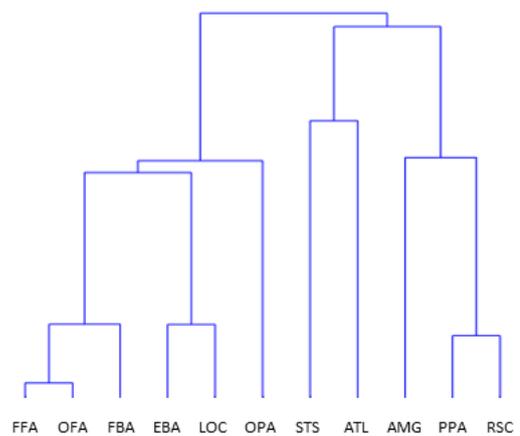


Figure 3 (A) Within-group and between group inter-subject correlations in category-selective (face, place, object, body) regions of visual cortex. There was no effect of group in any region. (B) Intra-subject correlations in the time-courses of response across all category-selective regions. (C) Hierarchical clustering of the data showing regions that have similar time-courses of response.

Whole Brain Analysis

Finally, we performed a whole-brain analysis using the 55 regions from the Harvard-Oxford atlas. The magnitude of the ISC varied across regions (Region: $F(54, 917) = 148, p < 0.0001$). Consistent with the previous analyses, the highest correlations were evident in regions of the occipital (lingual: $r = 0.39 \pm 0.01$, intracalcarine: $r = 0.33 \pm 0.01$) and temporal (posterior superior temporal: $r = 0.47 \pm 0.01$, occipital fusiform: $r = 0.37 \pm 0.01$, anterior superior temporal: $r = 0.35 \pm 0.01$) lobes.

Next, we asked whether there were group differences in the ISC. We found significantly higher ISC between individuals of the same group compared to individuals from different groups (Group: $F(1, 16) = 7.3, p < 0.05$). We also found that the difference between within-group and between-group correlations was greater in some regions compared to other regions (Region * Group interaction: $F(54, 918) = 2.8, p < 0.0001$). To determine which regions showed greater within-group correlations, we performed post-hoc t-tests in each of the 55 regions. 14 regions showed significantly higher within-group compared to between-group ISC (Fig. 4A): nucleus accumbens ($t(17) = 4.83, p < 0.0001$), pallidum ($t(17) = 4.39, p < 0.0005$), juxtapositional lobule ($t(17) = 4.28, p < 0.0005$), anterior cingulate ($t(17) = 3.66, p < 0.001$), putamen ($t(17) = 3.41, p < 0.005$), hippocampus ($t(17) = 3.03, p < 0.005$), insula ($t(17) = 2.90, p < 0.005$), anterior temporal fusiform ($t(17) = 2.89, p < 0.01$), frontal medial ($t(17) = 2.75, p < 0.01$), precentral gyrus ($t(17) = 2.63, p < 0.01$), posterior cingulate ($t(17) = 2.63, p < 0.01$),

frontal operculum ($t(17)= 2.40, p<0.05$), thalamus ($t(17)= 2.08, p<0.05$), paracingulate ($t(17)= 2.05, p<0.05$). When the Bonferroni-Holm method was applied to correct for multiple comparisons, 4 regions: nucleus accumbens ($p<0.005$), pallidum ($p<0.05$), juxtapositional lobule ($p<0.05$) and anterior cingulate ($p<0.05$) showed significant group differences.

To determine the connectivity between regions that showed a group bias, we compared the time-series of response between these regions within participants (Fig. 4B). These intra-subject correlations showed significant variation (range: 0.001 – 0.824). To determine the similarity between regions, hierarchical clustering was performed on the data (Fig. 4C). This shows that some regions showed more similar patterns of response than others. For example, regions in the basal ganglia (accumbens, putamen and pallidum) were highly correlated with each other ($r = 0.71 \pm 0.06$). Similarly, regions in cingulate cortex (anterior cingulate, posterior cingulate, paracingulate) also showed high correlations ($r = 0.74 \pm 0.03$). However, much lower correlations were evident between these two groups of regions ($r = 0.44 \pm 0.03$).

The strength of the correlations between regions did not always follow anatomical proximity. For example, the correlation between the juxtapositional lobule and precentral gyrus ($r = 0.73$) was higher than the correlation between these regions and the neighbouring regions in the cingulate cortex (0.52 ± 0.04). Similarly, the paracingulate and fronto-medial regions are anatomically proximal and also show group differences. Nonetheless, the inter-regional correlation between the paracingulate and the fronto-medial region was much lower ($r=0.33$) than between the more anatomically distant putamen (0.47) or insula ($r = 0.52$). Interestingly, not all regions showing a group bias showed strong interconnectivity. For

example, the frontal medial region showed very low correlations with the other 13 regions (0.12 ± 0.03).

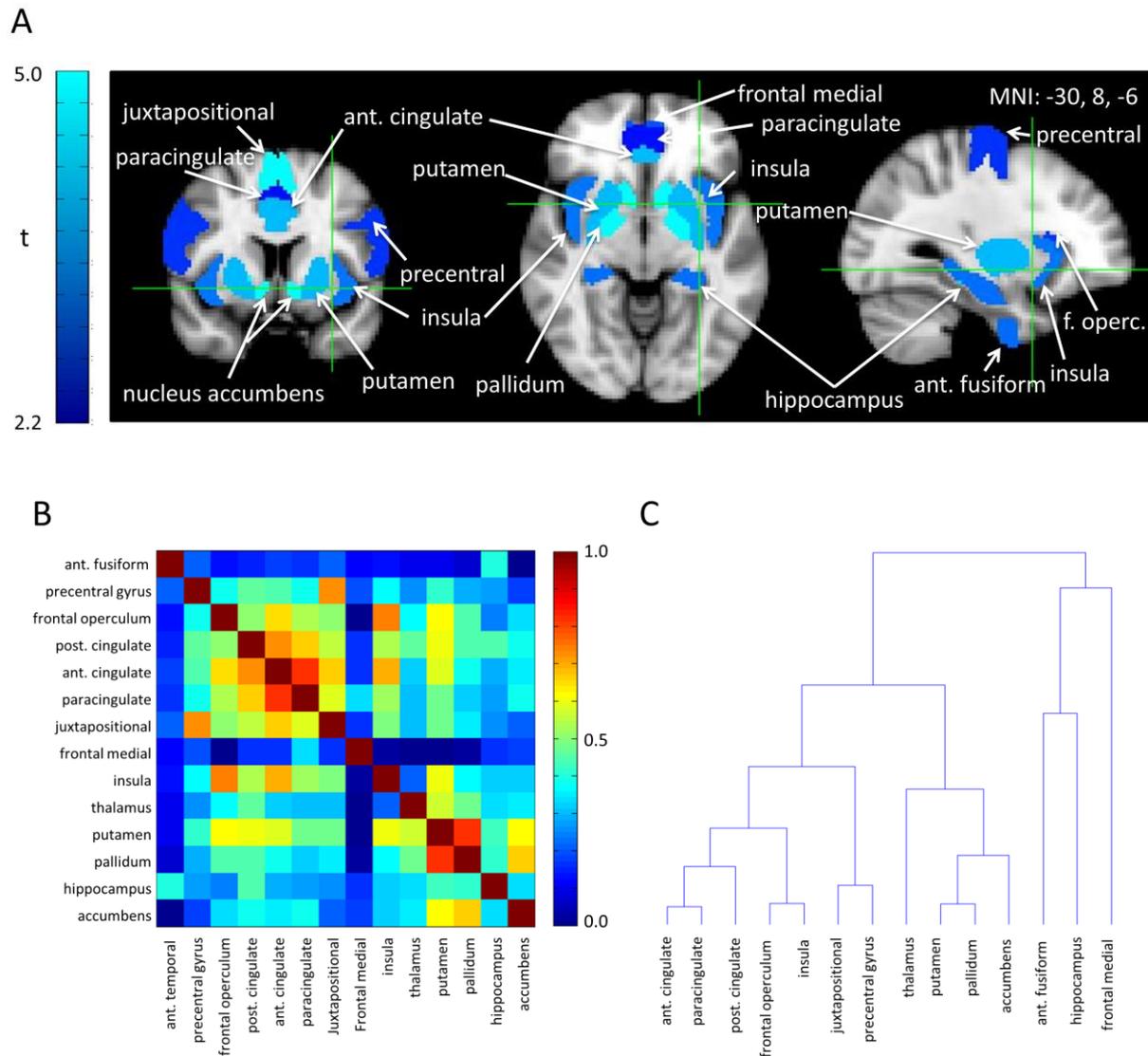


Figure 4 (A) Regions that showed higher within-group compared to between-group correlations. (B) Intra-subject correlations in the time-courses of response for all regions that showed a higher within-group correlations. (C) Hierarchical clustering of the data showing regions that have similar time-courses of response.

Our final analysis compared the similarity of the spatial pattern of response across the 55 regions at each time point. For each participant, we correlated the spatial pattern of response across the 55 regions at each time-point with the corresponding spatial pattern of response in a different participant (Fig. 5A). We then calculated a t-value for the within-group and between-group correlations across all time points for each group separately (Fig. 5B). We then asked whether the pattern of t-values across time from the two groups was different. There was a significant negative correlation ($r = -0.29$, $p < 0.00001$) showing that higher t-values for one group coincided with lower t-values in the other group. This demonstrates group differences in the spatial pattern of response across time.

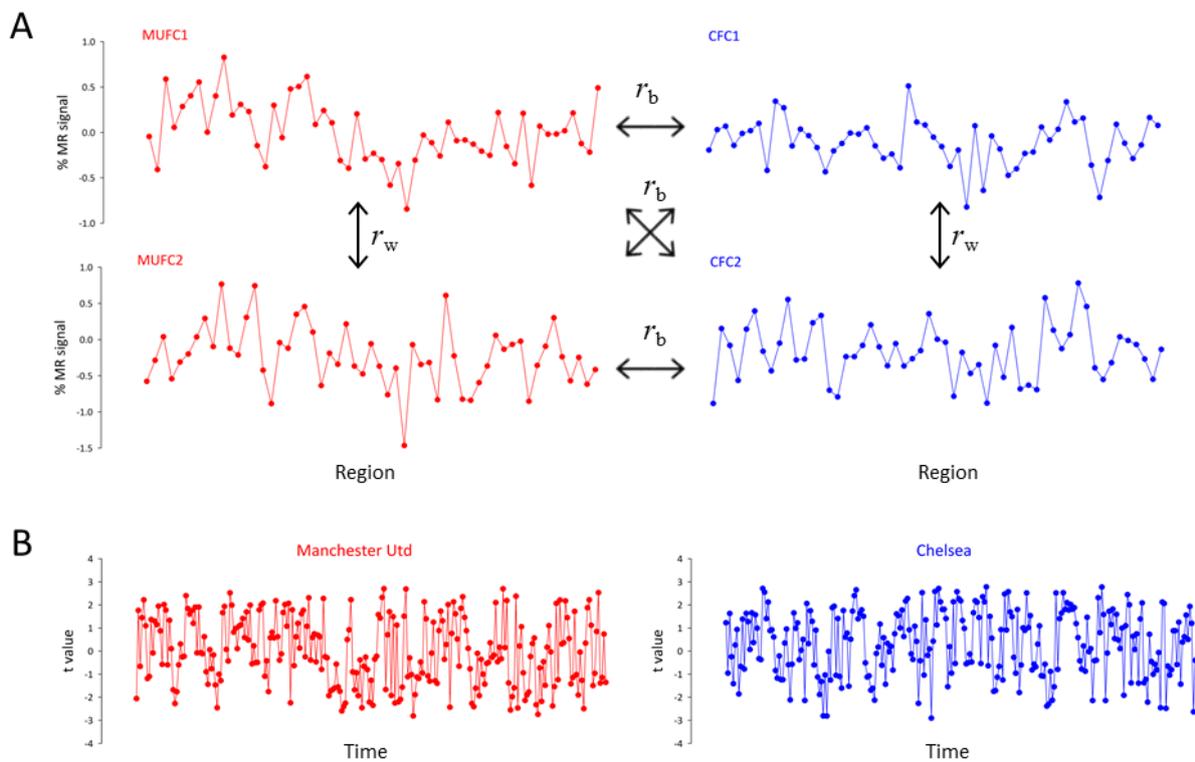


Figure 5 (A) Spatial patterns of response were compared by taking the response at each Region (55 regions of the Harvard-Oxford atlas) at one time-point from one individual and correlating this with the corresponding spatial pattern from a different individual from

either the same group (within-group, r_w) or with an individual from a different group (between-group, r_b). This process was repeated across all combinations of within- and between-group comparisons and a t-value calculated at each time-point. (B) The difference between the within-group and between-group comparisons in the spatial pattern at each time-point calculated independently for supporters of Manchester United (MUFC) and Chelsea (CFC). There was a significant negative correlation ($r = -0.29$, $p < 0.00001$) between the time-course of t-values from the two groups, demonstrating a group difference in the spatial pattern of response across time.

DISCUSSION

The aim of this study was to explore the neural correlates of social group bias during natural viewing. Participants in each social group were supporters of rival football teams and the natural viewing scenario involved watching a movie of games between the two teams. To determine group bias, we correlated the time-course of the neural response across participants. High inter-subject correlations (ISC) were evident in sensory regions of the occipital and temporal lobe, but these ISC did not vary as a function of group membership. In contrast, a number of frontal and subcortical regions showed significant group bias. That is, the ISC in these regions were higher for participants from the same group compared to participants from different groups.

The central question in this study is whether the neural correlates of group bias occur at an early or late stage of processing. In Hastorf and Cantril's study (1954), they concluded that individuals from both groups had watched a totally different game. However, it is not clear whether this difference was reflected in the way sensory information was represented or whether it reflected differences in the way the same sensory information was interpreted. We found the highest ISC in low-level and high-level visual areas in the occipital and temporal lobe. The strong ISC shows that, despite the completely free viewing of dynamic and complex stimulus, individual brains responded in a similar way. These findings are consistent with previous studies using these methods, which have shown that the highest ISC occur in these regions (Hasson et al., 2004; Hasson et al., 2010). However, in our study these regions did not show any within-group compared to between-group differences. This suggests that the sensory encoding of the stimulus was similar for both groups of participants. In other words, they saw the same game.

Regions that showed the greatest differences between groups were found in frontal and subcortical regions of the brain. Presumably, these differences reflect the differences in the interpretation of the movie in the two groups. For example, positive parts of the movie for one group are interpreted as negative by the other group. The idea that group differences are reflected in regions of the brain involved in the interpretation and understanding of the movie is consistent with previous studies that compared ISC for movies that vary in their narrative structure. For example, an unedited video of a concert, taken from a fixed viewpoint resulted in significant ISC in early visual and auditory areas, but little ISC in non-sensory regions of the brain (Hasson, Malach, & Heeger, 2010). However, more wide-spread ISC are evident in frontal regions with stronger narrative structures (Golland et al., 2007; Hasson et al., 2010; Jaaskelainen et al., 2008). The strong narrative structures presumably guide the interpretation of the movie in a way that is consistent across individuals.

Many of the regions that showed group bias have been implicated with the reward system (Haber & Knutson, 2010; Olds & Milner, 1954; Schultz, 2000). Although several brain regions are part of this circuit, the nucleus accumbens appears to play a central role. Interestingly, the region with the greatest group differences in our study was the nucleus accumbens. Our findings are consistent with other studies that have shown group differences in the neural response of the nucleus accumbens (Cikara et al., 2011; Hein et al., 2010). The reward network also includes regions such as the cingulate cortex, medial prefrontal regions, pallidum, thalamus, insula and the hippocampus (Haber & Knutson, 2010). Many of these regions also showed a group bias in the current study. The link between group differences and the brain's reward system may explain the ease and rapidity with which humans form groups and favour in-group members (Tajfel, 1982; Turner et al., 1987)

Not all regions that showed group bias are directly involved in the reward system. For example, regions that are typically associated with motor control such as the juxtapositional lobule (supplementary motor cortex) and the precentral gyrus also showed higher within-group correlations. This fits with differences in the neural response of motor areas that are evident when observing the movements of in-group and out-group members (Avenanti, Sirigu, & Aglioti, 2010; Gutsell & Inzlicht, 2010). This suggests that we experience the actions of in-group and out-group members differently. The activation of motor regions during the perception of movement has been suggested as a mechanism by which people understand the intentions and emotions of others (de Waal & Preston, 2017). Together, these results suggest that this mechanism may play a role in-group differences in behaviour. We also found group differences in the insula (see Hein et al., 2010), frontal operculum and the hippocampus suggesting importance of affective processing and memory in group differences.

To investigate how the network of areas showing a group bias were interconnected, we compared the time course of response between regions within participants (intra-subject correlation). We found highly correlated responses among subcortical regions (nucleus accumbens, pallidum, putamen) or among regions in cingulate cortex (anterior cingulate, posterior cingulate, paracingulate), but lower correlations between these groups of regions. The frontal medial region showed the lowest correlations with the other regions showing group differences. Midline structures in the cingulate and medial frontal cortex are thought to play an important role in social cognition, particularly in the ability to attribute mental states to others (Blakemore, 2008; Frith, 2007). These results suggest a dissociation in the processing within these regions.

There were a few regions that did not show any group differences despite the fact that they have been implicated in previous studies of group differences. For example, previous studies have found group differences in the amygdala and the TPJ (Cunningham et al., 2004; Hart et al., 2000; Phelps et al., 2000; Wheeler & Fiske, 2005; Van Bavel et al., 2008; Cheon et al., 2011; Freeman et al., 2010). It is not clear why we did not find any group differences in these regions. This may reflect the differences in paradigms between studies. These studies typically involve tasks that involve making explicit judgements in relation to in-group or out-group members. They also measure the magnitude of the neural response within individuals. In contrast, our paradigm attempts to immerse participants into a natural viewing environment that simulates a group experience, but without having to make any explicit judgement of the events. Moreover, our method of analysis compares similarity in the time-course of response across individuals.

The final analysis investigated the spatial pattern of response across the brain at each time point. This was calculated separately for the two groups to generate a time-course of t-values showing group differences in the spatial pattern of response across time. We compared these time-courses and found that there was a significant negative correlation. This shows that group differences in the spatial patterns of response occurred at different times in the two groups, which again demonstrates differences in the way that different parts of the video were interpreted.

In conclusion, this study investigated the neural correlates of group differences during natural viewing. We found that sensory regions in the occipital and temporal regions of the brain showed high inter-subject correlations. However, these regions did not show any group differences. In contrast, frontal and subcortical regions showed significant group differences.

The interactions between these regions suggests that group bias does not reflect a single mechanism, but rather a range of cognitive processes from the control of movement to social cognition and reward.

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