ORIGINAL ARTICLE

Neural Correlates of Group Bias During Natural Viewing

Timothy J. Andrews ⓘ , Ryan K. Smith, Richard L. Hoggart, Philip I. N. Ulrich and Andre D. Gouws

Department of Psychology, University of York, York, YO10 5DD, UK

Address correspondence to Timothy J. Andrews. Email: timothy.andrews@york.ac.uk ⓘ orcid.org/0000-0001-8255-9120

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 2 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 intersubject 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.

Key words: fMRI, in-group, ISC, natural viewing, nucleus accumbens

Introduction

Our perception of the world is influenced by the presence of others (Allport 1954; Asch 1955; Milgram 1974; Cialdini and Goldstein 2004). 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 et al. 1961; Amodio 2014; Xiao et al. 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 et al. 1987). A challenge to understanding group bias is revealing the specific cognitive and neural processes that give rise to differences in behavior. 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 et al. 2001; Lieberman et al. 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 (Hart et al. 2000; Cunningham et al. 2004). 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 and 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 (Freeman et al. 2010; Van Bavel et al. 2008, 2011; Amodio 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 et al. 2013).

It remains unclear, however, whether group differences in behavior are more associated with the way information is interpreted (Molenberghs 2013). For example, Cikara et al. (2011) found that positive in-group outcomes for baseball fans (success of the favored team or failure of the rival team) were correlated with activity in the ventral striatum. 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 (Richeson et al. 2003; Xu et al. 2009; Freeman et al. 2010; Hein et al. 2010; Mathur et al. 2010; Cheon et al. 2011, 2011). The flexibility of these regions is demonstrated by similar in-group bias when the groups are defined by the minimal group paradigm (Van Bavel et al. 2008; Volz et al. 2009; Morrison et al. 2012).

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 et al. (2004) developed a novel neuroimaging approach in which natural viewing conditions are simulated by presenting participants with movies. The data are analyzed by comparing the time-courses of response in corresponding regions across subjects. This approach has been used to show that there are significant intersubject correlations or similarities in the neural response, particularly in sensory regions of the occipital and temporal lobe (Hasson et al. 2004, 2010).

Here, we use the intersubject 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 2 sides. Our hypothesis was that brain regions that showed larger within-group compared with between-group intersubject correlations are associated with the cognitive processes evident in group bias.

Methods

Participants

A total of 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. Nine 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 intersubject correlation paradigm (Hasson et al. 2004, 2008). To ensure that strong group biases were evident, we recruited participants who had on average supported their team for over 15 years (mean ± standard error of the mean (SEM): 15.2 ± 1.2) and had attended over 25 games (mean ± SEM: 25.6 ± 14.0). Written consent was obtained for all participants and the study was approved by the York Neuroimaging Center 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 s (range: 9–39 s). 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 Center (YNiC) using a GE 3 T HDx Excite MRI scanner. A Magnex head-dedicated gradient insert coil was used in conjunction with a birdcage, radiofrequency coil tuned to 127.7 MHz. Data were collected from 38 contiguous axial slices via a gradient-echo EPI sequence (TR = 3 s, TE = 32.5 ms, FOV = 288 × 288 mm^2, matrix size = 128 × 128, voxel dimensions = 2.25 × 2.25 mm^2, 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 × 288 mm^2, matrix size = 512 × 512, voxel dimensions = 0.56 × 0.56 mm^2, 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 × 290 mm^2, matrix size = 256 × 256, voxel dimensions = 1.13 × 1.13 mm^2, slice thickness = 1 mm, flip angle = 20).

The fMRI data were analyzed with FEAT v5.98 (http://www.fmrib.ox.ac.uk/fsl). In all scans the initial 9 s 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 = 50 s). Spatial smoothing (Gaussian) was applied at 6 mm FWHM. Functional data were first registered to a high-resolution T1-anatomical image and then onto the standard MNI brain (ICBM152).

fMRI Analysis

To analyze 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 3 different methods. First, we compared responses in early visual areas using the probabilistic masks based on visual field maps developed by 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 (Davies-Thompson et al.

2012). Images from each condition were presented in a blocked-design. Overall, 10 images (each image was presented for 700 ms with a 200 ms ISI) were presented in each block and a 9 s gray fixation screen was presented between blocks. Each condition was presented 4 times in a pseudorandomized 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 with 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 $Z > 2.3$ (Supplementary Fig. S1). 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 and 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.

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 analyzed 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 analyze the data. Post hoc t-tests were then used to determine which regions showed significantly higher within-group compared with between-group correlations.

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 intersubject 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 interconnected a hierarchical clustering analysis was performed (https://www.mathworks.com) using an unweighted average distance method for computing the distance between clusters and 1 – 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 intrasubject correlations, there were no significant group differences in the ISC.

Category-Selective Regions

Next, we compared ISC 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 interconnected 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 intrasubject correlations show that category-selective networks have distinct time-courses of response. Nevertheless, the ISC 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 2 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 nonpreferred 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.
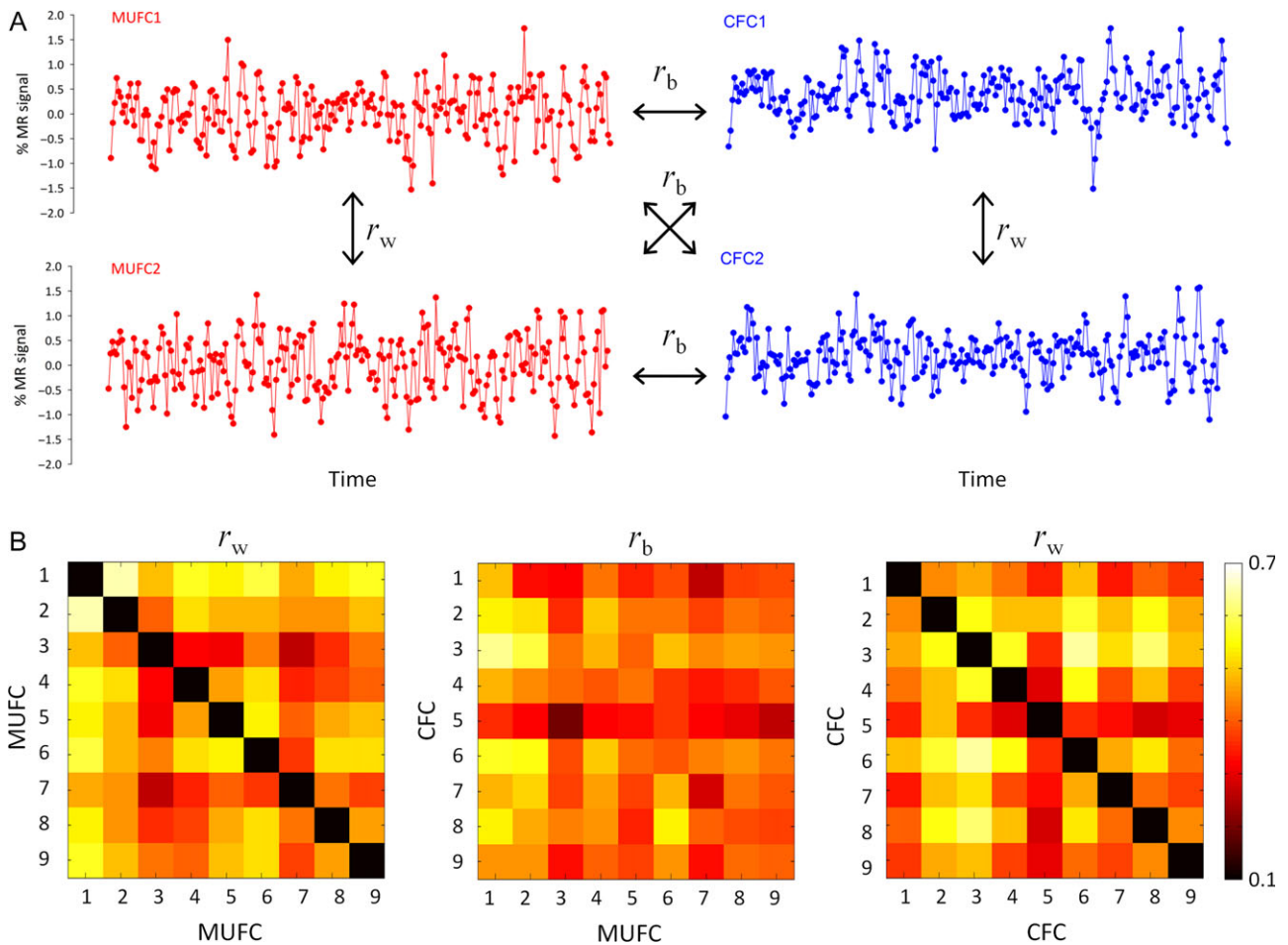
Figure 1. Within-group and between-group intersubject correlations (ISC) from one brain region. (A) ISC were measured by taking the time-course of neural response from one individual and correlating this with the corresponding time-course from a different individual from the same group (within-group, 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.

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 with 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 with 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. The 14 regions showed significantly higher within-group compared with 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 intrasubject 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 2 groups of regions ($r = 0.44 \pm 0.03$).

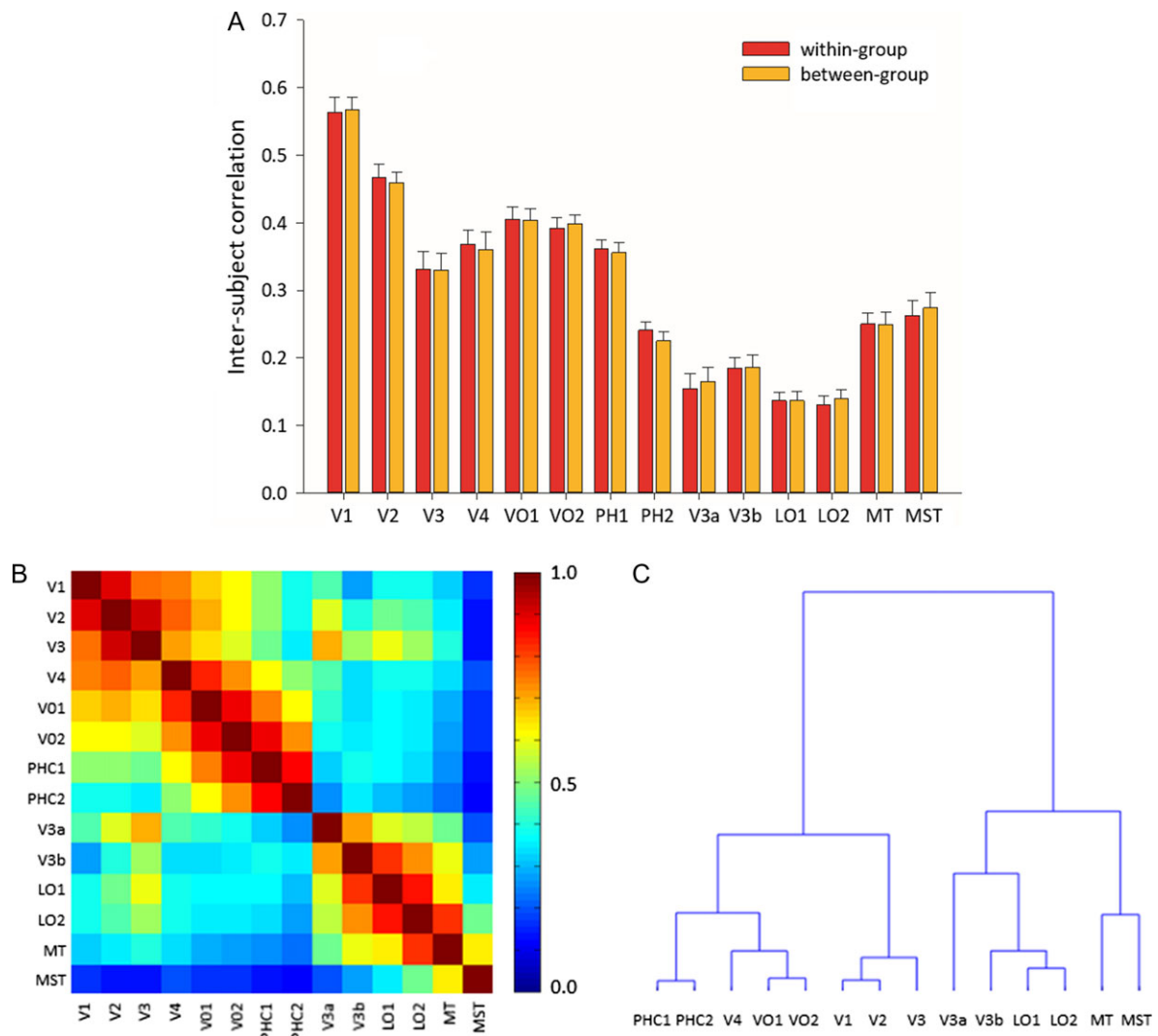The strength of the correlations between regions did not always follow anatomical proximity. For example, the

Figure 2. (A) Within-group and between group intersubject correlations in visual field regions. There was no effect of group in any region. (B) Intrasubject 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.

correlation between the juxtapositional lobule and precentral gyrus ($r = 0.73$) was higher than the correlation between these regions and the neighboring regions in the cingulate cortex (0.52 ± 0.04). Similarly, the paracingulate and frontomedial regions are anatomically proximal and also show group differences. Nonetheless, the inter-regional correlation between the paracingulate and the frontomedial region was much lower ($r = 0.33$) than between the more anatomically distant putamen (0.47) or insula (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).

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 2 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.

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 2 teams. To determine group bias, we correlated the time-course of the neural response across participants. High 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 with 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
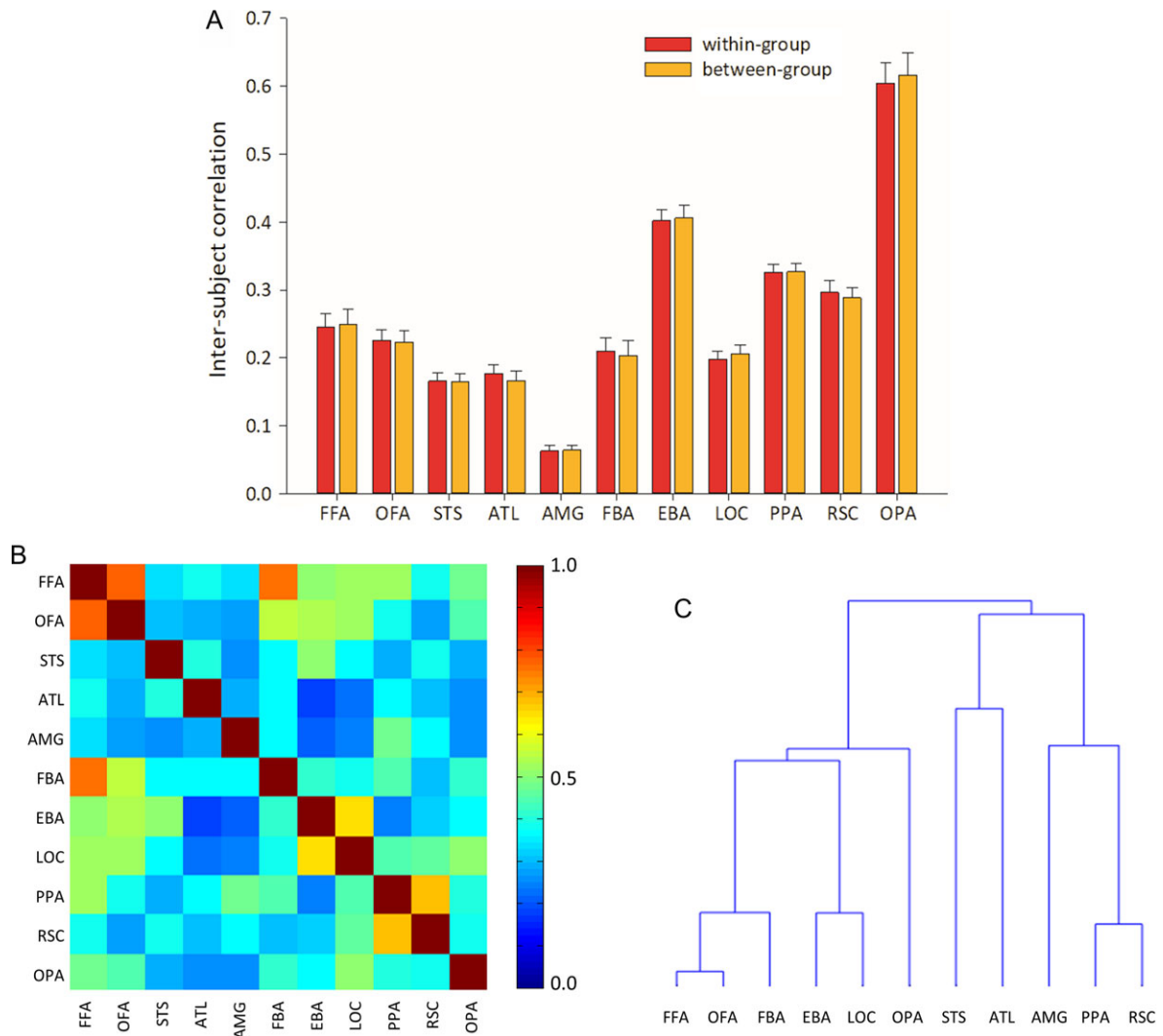
Figure 3. (A) Within-group and between group intersubject correlations in category-selective (face, place, object, body) regions of visual cortex. There was no effect of group in any region. (B) Intrasubject correlations in the time-courses of response across all category-selective regions. (C) Hierarchical clustering of the data showing regions that have similar time-courses of response.

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, 2010). However, in our study these regions did not show any within-group compared with 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 2 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 nonsensory regions of the brain (Hasson et al. 2010). However, more widespread ISC are evident in frontal regions with stronger narrative structures (Golland et al. 2007; Jaaskelainen et al. 2008; Hasson et al. 2010). 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 (Olds and Milner 1954; Schultz 2000; Haber and Knutson 2010). 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
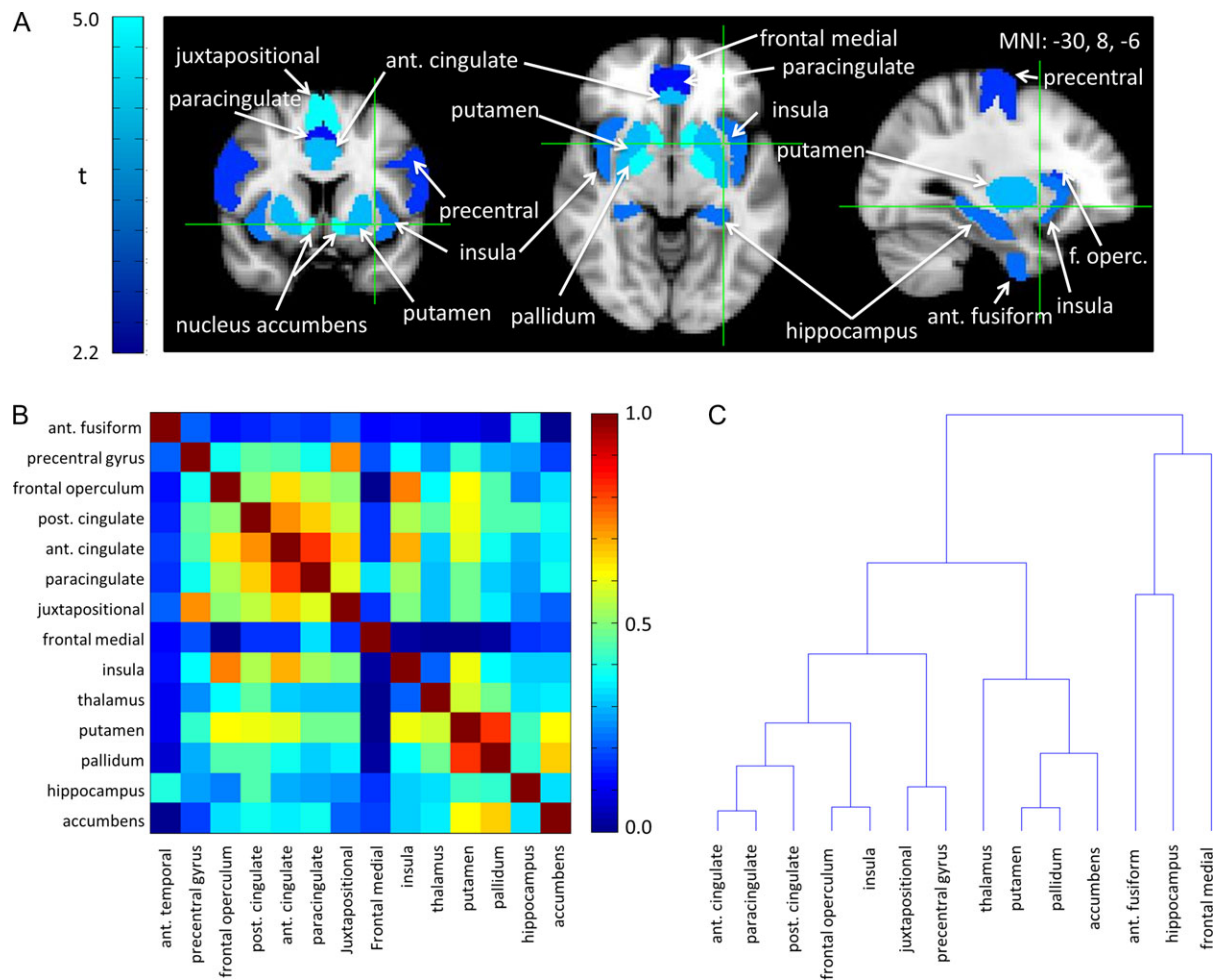
Figure 4. (A) Regions that showed higher within-group compared with between-group correlations. (B) Intrasubject correlations in the time-courses of response for all regions that showed a higher within-group correlations. (C) Hierarchical clustering of the data showing regions that have similar time-courses of response.

group differences in the neural response of the nucleus accumbens (Hein et al. 2010; Cikara et al. 2011). The reward network also includes regions such as the cingulate cortex, medial prefrontal regions, pallidum, thalamus, insula, and the hippocampus (Haber and 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 favor 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 et al. 2010; Gutsell and 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 and Preston 2017). Together, these results suggest that this mechanism may play a role in-group differences in behavior. We also found group differences in the insula (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 (intrasubject correlation). We found highly correlated responses among subcortical regions (nucleus accumbens, palidum, 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 (Frith 2007; Blakemore 2008). 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 (Hart et al. 2000; Phelps et al. 2000; Cunningham et al. 2004; Wheeler and Fiske 2005; Van Bavel et al. 2008; Freeman et al. 2010; Cheon et al. 2011). 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
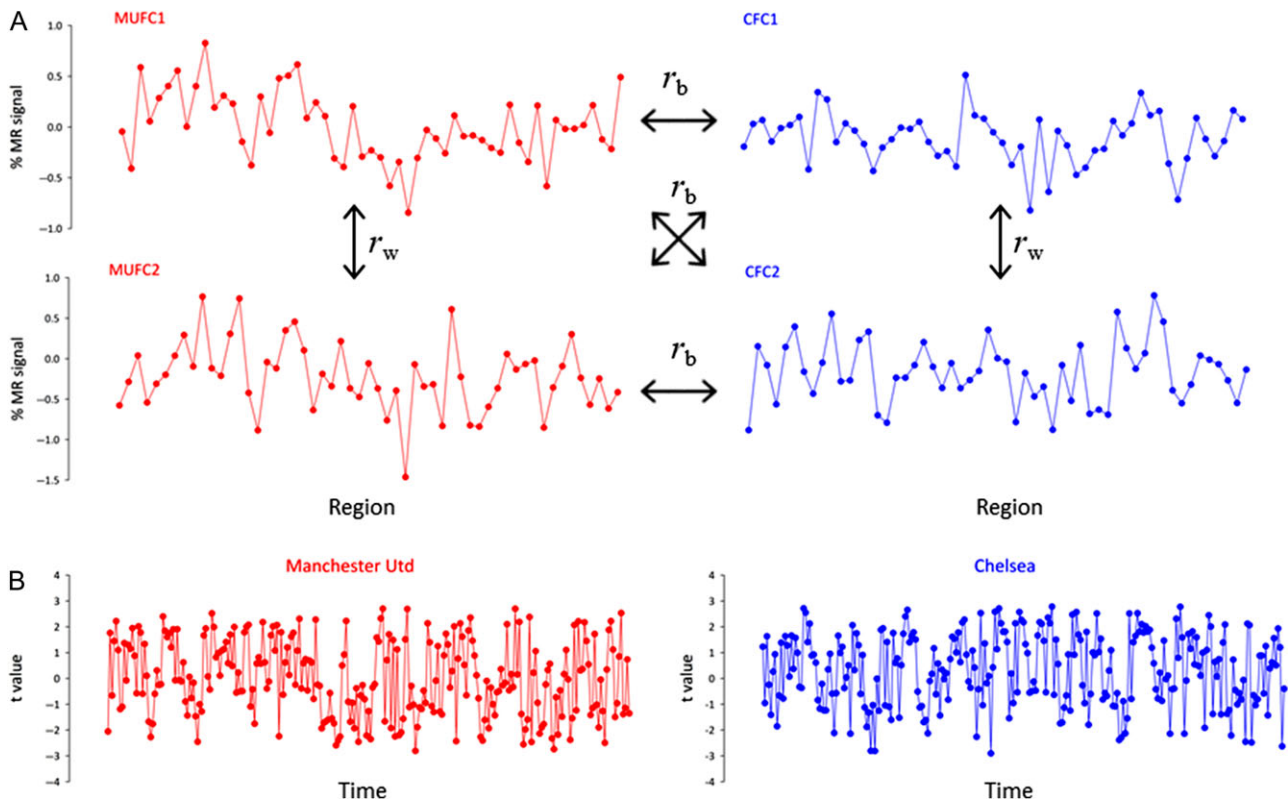
Figure 5. (A) Spatial patterns of response were compared by taking the response at each region (55 regions of the Harvard-Oxford atlas) at one time-point from one individual and correlating this with the corresponding spatial pattern from a different individual from either the same group (within-group, 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 2 groups, demonstrating a group difference in the spatial pattern of response across time.

involve tasks that involve making explicit judgments 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 judgment 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 2 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 2 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 ISC. 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.

Supplementary Material

Supplementary material is available at *Cerebral Cortex* online.

Notes

References

Allport GW. 1954. The nature of prejudice. Cambridge, Mass.: Addison-Wesley Pub. Co.

Amodio DM. 2014. The neuroscience of prejudice and stereotyping. Nat Rev Neurosci. 15:670–682.

Andrews TJ. 2005. Visual cortex: how are objects and faces represented? Curr Biol. 15:451–453.

Asch SE. 1955. Opinions and social pressure. Sci Am. 193(5): 31–35.

Avenanti A, Sirigu A, Aglioti SM. 2010. Racial bias reduces empathic sensorimotor resonance with other-race pain. Curr Biol. 20(11):1018–1022. doi:10.1016/j.cub.2010.03.071.

Blakemore SJ. 2008. The social brain in adolescence. Nat Rev Neurosci. 9(4):267–277. doi:10.1038/nrn2353.

Cheon BK, Im DM, Harada T, Kim JS, Mathur VA, Scimeca JM, Chiao JY. 2011. Cultural influences on neural basis of intergroup empathy. Neuroimage. 57:642–650.

Cialdini RB, Goldstein NJ. 2004. Social influence: compliance and conformity. Annu Rev Psychol. 55:591–621. doi:10.1146/annurev.psych.55.090902.142015.

Cikara M, Botvinick MM, Fiske ST. 2011. Us versus them: social identity shapes neural responses to intergroup competition and harm. Psychol Sci. 22(3):306–313. doi:10.1177/0956797610397667.

Cikara M, Van Bavel JJ. 2014. The neuroscience of intergroup relations: an integrative review. Perspect Psychol Sci. 9(3): 245–274.

Cunningham WA, Johnson MK, Raye CL, Gatenby JC, Gore JC, Banaji MR. 2004. Separable neural components in the processing of black and white faces. Psychol Sci. 15(12):806–813. doi:10.1111/j.0956-7976.2004.00760.x.

Davies-Thompson J, Andrews TJ. 2012. Intra- and interhemispheric connectivity between face-selective regions in the human brain. J Neurophysiol 108:3087–3095.

de Waal FBM, Preston SD. 2017. Mammalian empathy: behavioural manifestations and neural basis. Nat Rev Neurosci. 18(8):498–509. doi:10.1038/nrn.2017.72.

Downing PE, Jiang Y, Shuman M, Kanwisher N. 2001. A cortical area selective for visual processing of the human body. Science. 293(5539):2470–2473.

Epstein R, Kanwisher N. 1998. A cortical representation of the local visual environment. Nature. 392(6676):598–601.

Ewbank MP, Schluppeck D, Andrews TJ. 2005. FMR-adaptation reveals a distributed representation of inanimate objects and places in human visual cortex. Neuroimage. 28:268–279.

Freeman JB, Schiller D, Rule NO, Ambady N. 2010. The neural origins of superficial and individuated. Hum Brain Mapp. 31: 150–159.

Frith CD. 2007. The social brain? Philos Trans R Soc Lond B Biol Sci. 362(1480):671–678. doi:10.1098/rstb.2006.2003.

Golby AJ, Gabrieli JD, Chiao JY, Eberhardt JL. 2001. Differential responses in the fusiform region to same-race and other-race faces. Nat Neurosci. 4(8):845–850. doi:10.1038/90565.

Golland Y, Bentin S, Gelbard H, Benjamini Y, Heller R, Nir Y, Hasson U, Malach R. 2007. Extrinsic and intrinsic systems in the posterior cortex of the human brain revealed during natural sensory stimulation. Cereb Cortex. 17(4):766–777. doi:10.1093/cercor/bhk030.

Gutsell JN, Inzlicht M. 2010. Empathy constrained: prejudice predicts reduced mental simulation of actions during observation of outgroups. J Exp Soc Psychol. 46(5):841–845. doi:10.1016/j.jesp.2010.03.011.

Haber SN, Knutson B. 2010. The reward circuit: linking primate anatomy and human imaging. Neuropsychopharmacology. 35(1):4–26. doi:10.1038/npp.2009.129.

Hart AJ, Whalen PJ, Shin LM, McInerney SC, Fischer H, Rauch SL. 2000. Differential response in the human amygdala to racial outgroup vs ingroup face stimuli. Neuroreport. 11(11): 2351–2355. doi:10.1097/00001756-200008030-00004.

Hasson U, Malach R, Heeger DJ. 2010. Reliability of cortical activity during natural stimulation. Trends Cogn Sci. 14(1): 40–48. doi:10.1016/j.tics.2009.10.011.

Hasson U, Nir Y, Levy I, Fuhrmann G, Malach R. 2004. Intersubject synchronization of cortical activity during natural vision. Science. 303(5664):1634–1640. doi:10.1126/science.1089506.

Hasson U, Yang E, Vallines I, Heeger DJ, Rubin N. 2008. A hierarchy of temporal receptive windows in human cortex. J Neurosci. 28(10):2539–2550. doi:10.1523/JNEUROSCI.5487-07.2008.

Hastorf AH, Cantril H. 1954. They saw a game: a case study. J Abnorm Psychol. 49(1):129–134.

Hein G, Silani G, Preuschoff K, Batson CD, Singer T. 2010. Neural responses to ingroup and outgroup members' suffering predict individual differences in costly helping. Neuron. 68(1): 149–160. doi:10.1016/j.neuron.2010.09.003.

Ishai A, Ungerleider LG, Martin A, Schouten JL, Haxby JV. 1999. Distributed representation of objects in the human ventral visual pathway. Proc Natl Acad Sci USA. 96:9379–9384.

Jaaskelainen IP, Koskentalo K, Balk MH, Autti T, Kauramaki J, Pomren C, Sams M. 2008. Inter-subject synchronization of prefrontal cortex hemodynamic activity during natural viewing. Open Neuroimag J. 2:14–19. doi:10.2174/1874440000802010014.

Kanwisher N, McDermott J, Chun MM. 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. J Neurosci. 17(11):4302–4311.

Lieberman MD, Hariri A, Jarcho JM, Eisenberger NI, Bookheimer SY. 2005. An fMRI investigation of race-related amygdala activity in African-American and Caucasian-American individuals. Nat Neurosci. 8(6):720–722. doi:10.1038/nn1465.

Malach R, Reppas JB, Benson RR, Kwong KK, Jiang H, Kennedy WA, Ledden PJ, Brady TJ, Rosen BR, Tootell RB. 1995. Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. Proc Natl Acad Sci USA. 92:8135–8139.

Mathur VA, Harada T, Lipke T, Chiao JY. 2010. Neural basis of extraordinary empathy and altruistic motivation. Neuroimage. 51(4):1468–1475. doi:10.1016/j.neuroimage.2010.03.025.

Milgram S. 1974. Obedience to authority; an experimental view. 1st ed. New York: Harper & Row.

Molenberghs P. 2013. The neuroscience of in-group bias. Neurosci Biobehav Rev. 37(8):1530–1536. doi:10.1016/j.neubiorev.2013.06.002.

Molenberghs P, Halasz V, Mattingley JB, Vanman EJ, Cunnington R. 2013. Seeing is believing: neural mechanisms of action-perception are biased by team membership. Hum Brain Mapp. 34(9):2055–2068. doi:10.1002/hbm.22044.

Morrison S, Decety J, Molenberghs P. 2012. The neuroscience of group membership. Neuropsychologia. 50(8):2114–2120. doi:10.1016/j.neuropsychologia.2012.05.014.

Olds J, Milner P. 1954. Positive reinforcement produced by electrical stimulation of septal area and other regions of rat brain. J Comp Physiol Psychol. 47(6):419–427.

Phelps EA, O'Connor KJ, Cunningham WA, Funayama ES, Gatenby JC, Gore JC, Banaji MR. 2000. Performance on indirect measures of race evaluation predicts amygdala activation. J Cogn Neurosci. 12(5):729–738.

Richeson JA, Baird AA, Gordon HL, Heatherton TF, Wyland CL, Trawalter S, Shelton JN. 2003. An fMRI investigation of the impact of interracial contact on executive function. Nat Neurosci. 6(12):1323–1328. doi:10.1038/nn1156.

Schultz W. 2000. Multiple reward signals in the brain. Nat Rev Neurosci. 1(3):199–207. doi:10.1038/35044563.

Sherif M, Harvey OJ, White BJ, Hood WR, Sherif CW. 1961. The Robbers Cave experiment: intergroup conflict and cooperation.

Tajfel H. 1982. Social-psychology of inter-group relations. Annu Rev Psychol. 33:1–39. doi:10.1146/annurev.ps.33.020182.000245.

Turner JC, Hogg MA, Oakes PJ, Reicher SD, Wetherell MS. 1987. Rediscovering the social group: a self-categorization theory. Oxford: Blackwell.

Van Bavel JJ, Packer DJ, Cunningham WA. 2008. The neural substrates of in-group bias: a functional magnetic resonance imaging investigation. Psychol Sci. 19(11):1131–1139. doi:10.1111/j.1467-9280.2008.02214.x.

Van Bavel JJ, Packer DJ, Cunningham WA. 2011. Modulation of the Fusiform Face Area following minimal exposure to motivationally relevant faces: evidence of ingroup enhancement (not out-group disregard). J Cogn Neurosci. 23:3343–3354. doi:10.1162/jocn_a_00016.

Volz KG, Kessler T, von Cramon DY. 2009. In-group as part of the self: in-group favoritism is mediated by medial prefrontal cortex activation. Soc Neurosci. 4(3):244–260. doi:10.1080/17470910802553565.

Wang L, Mruczek REB, Arcaro MJ, Kastner S. 2015. Probabilistic maps of visual topography in human cortex. Cereb Cortex. 25(10):3911–3931.

Wheeler ME, Fiske ST. 2005. Controlling racial prejudice: social-cognitive goals affect amygdala and stereotype activation. Psychol Sci. 16(1):56–63. doi:10.1111/j.0956-7976.2005.00780.x.

Xiao YJ, Coppin G, Van Bavel JJ. 2016. Perceiving the world through group-colored glasses: a perceptual model of intergroup relations. Psychol Inq. 27(4):255–274. doi:10.1080/1047840x.2016.1199221.

Xu X, Zuo X, Wang X, Han S. 2009. Do you feel my pain? Racial group membership modulates empathic neural responses. J Neurosci. 29:8525–8529.