**Changes in intrinsic functional connectivity and group relevant salience: The case of sport rivalry**

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Previous studies have shown that the social associations we have with a stimulus can modulate attention and perception. Here we present novel evidence that social associations relating to in- and outgroup membership lead to rapid changes in functional connectivity in the brain, altering the brain’s intrinsic connectivity between brain regions associated with social salience, emotion and cognitive control. Moreover, these changes in intrinsic connectivity correlate positively with in-group biases in behavior. These findings indicate that in-group bias is associated with rapid changes in intrinsic connectivity in a neural network signaling the social and emotional salience of stimuli.

Whether watching a football match involving a favourite team, recognizing the voice of a friend in a noisy environment or smelling the perfume of a loved one at a party, the brain is involved in processing socially relevant information, which can stand out from other irrelevant information that is present *(1)*. There is now considerable evidence on the effects of social relevance on attention, memory, learning and decision making across different contexts *(2-5).* These findings indicate that social relevance can raise the salience of stimuli for perception and attention *(6-8)*, enhancing the processing of stimuli that are personally relevant - for example, objects associated to self *(4,9-10,15)*, a loved one *(11)* or one’s in-group *(12-14,16)*.

Historically research *(9-16)* has focused on personally familiar stimuli, whose social relevance is already learned. In contrast we have little knowledge about how new social associations are established and how this affects brain processing. This issue is of considerable importance if we are to understand how social biases are formed. Current evidence from magnetic resonance imaging (fMRI) studies across different domains using a variety of tasks suggests that the anterior insula (AI) is a key part of a neural network responding to subjective cognitive, emotional and social salience *(17).* Furthermore, clinical studies demonstrate the necessary role of this region since degeneration of fronto-insula cortex disrupts appropriate responses to socially salient stimuli *(18).* Here, in order to understand the way that new social associations are formed, we derived fMRI measures when (i) participants were at rest, (ii) they discriminated in-group associated stimuli and (iii) they were at rest again, and we focused on changes in intrinsic functional connectivity to the insula that took place between the two rest periods. Such changes reflect the neuro-plasticity of the brain in relation to in-group associations, and we evaluated the relations between these changes and biases to in-group items in a simple perceptual matching task. We asked whether functional changes in brain connectivity predict in-group biases in cognition.

We used a novel social association learning task with twenty passionate football fans. Participants learnt to associate simple geometric shapes with the badges of their favourite football team (the in-group), its closest rival and a neutral team (the out-groups). Subsequently they viewed different pairs of badges and shapes and they were asked to indicate whether the pairing was correct or incorrect based on the original associations. Brain imaging was conducted prior to participants performing the perceptual matching task, during the matching task and then when at rest after matching the stimuli.

We applied a two-stage analysis approach. First, we selected regions of interest (ROIs) using the areas activated during the social association task. Second, we used these ROIs as seeds to explore the changes in resting state functional connectivity before and after the social association task was performed. By comparing resting state activity before and after the task, we evaluated changes in underlying functional activity controlling for individual differences at baseline. We predicted that the football fans would show enhanced behavioral performance for in-group stimuli compared to stimuli associated to out-groups (*16*). Further, we predicted this enhanced performance would be linked to activity in insula cortex.

A general linear model analysis of the functional data collected during the social association task revealed statistically significant (*p<0.005*, minimal cluster size 70 voxels) activity in the left posterior superior temporal sulcus related to the responses to in-group associated stimuli compared to the rival out-group. In contrast, there was greater activity for rival over in-group associations within the dorsal attentional control network including the left dorsal prefrontal, superior medial and the inferior dorsal parietal cortex. There was also enhanced activity in the left anterior insula (AI). More details regarding the activation map in the task can be found in the supplementary materials. Figure 1 provides an example of the activation map in the fMRI task.

Figure 1. about here

From these activated areas six regions of interest (ROIs) were selected to enter into intrinsic functional connectivity analyses. These ROIs included the left AI, the left inferior frontal gyrus (IFG), the left dorsolateral prefrontal cortex (DLPFC), the left posterior superior temporal sulcus (pSTS), the left precuneus and the left fusiform gyrus.

We then compared and contrasted the strength of functional connectivity between the pairs of ROIs under resting state conditions before and after the task.

The significance level was corrected for multiple comparisons and only pairs with *p<.003* (.05/15) were counted as significant. Our results showed that, compared to the pre-task activity, the strength of functional connectivity between the left AI and the left inferior frontal gyrus (IFG) increased significantly, *t(19)*= 2.80, *p=.003*. Furthermore, there was a reliable decrease in the strength of functional connectivity between the left dorsolateral prefrontal cortex (DLPFC) and the left AI, *t(19)=* -3.34, *p<.0001*, in the post- compared to the pre-task condition. The results matrices for pre-task, post-task and for the post vs. pre-task are depicted in Figures 2a, 2b and 2c respectively.

Figure 2. about here

Next we tested the relations between functional connectivity and behavioral performance. To find any potential linkage we conducted correlational analyses on the strength of post-task functional connectivity (using the t-value of the post-task functional connectivity for each pair of ROIs) with the difference in RT for in-group vs. out-group stimuli in the task. Our results showed that the strength of the post-task functional connectivity between the left AI and left IFG was significantly correlated with the size of the in-group bias in reaction times, *r= .50, p=.024, N=20*. In contrast the correlation between the in-group bias and the DLPF/AI post-task functional connectivity was not reliable, *r= .061, p=.808, N=20*. There was also no correlation between the increase in the functional connectivity between (i) the IFG and the AI and (ii) the decrease in connectivity between the AI and the DLPFC, *r= .102, p=.661, N=20.* We also tested whether pre-task functional connectivity between AI and i) DLPFC and ii) IFG correlated with in-group bias. Our results showed that in-group bias was not significantly correlated with pre-task functional connectivity from the left AI to either i) the DLPFC, *r= .228, p=.334, N=20,* or ii) the IFG *r= .407, p=.075, N=20.* The results for the correlational analyses are shown in Figure 3.

Figure 3. about here

In this study we asked a fundamental question concerning whether learning new social associations causes rapid re-configuration in the brain. We assessed whether, in a group of passionate football fans, performance on a perceptual matching task using stimuli associated with an in- or out-group alters intrinsic functional connectivity in the brain, contrasting pre- vs. post-task resting state fMRI. Our results revealed that the strength of functional connectivity was significantly increased between the left AI and the IFG. Prior to learning, the functional connectivity did not vary between those showing large and those showing small behavioral biases. However the changes in functional connectivity after learning were related to the magnitude of the behavioral biases in the task. Notably there was a positive correlation between the changes in functional connectivity between (i) the left IFG and AI and (ii) the size of the in-group bias, based on the reaction time difference between in- and out-group stimuli. We further found a decrease in functional connectivity between the AI and the DLPFC post-task compared to pre-task, but this was unrelated to task performance.

The findings regarding the IFG and AI suggest that functional hyper- connectivity with a fronto-insula network is related to an enhanced contrast in perception for in- vs. out-group stimuli. Previous studies have reported evidence for functional connectivity between the IFG and the AI. For example, using Granger Causality it has been shown that activity in the IFG was associated with responses in the AI to emotional faces *(21).* Recent studies of the functional synchronization of activity between the AI and IFG further indicate that coherent co-activation of these areas arises across a wide variety of contexts consistent with the two regions acting as a “fronto-insula junction “in social and emotional processing *(22).* There is also anatomical evidence showing that within this fronto-insula system, the anterior insula is connected to the pars triangularis area of IFG (our selected seed BA 45) via one of the shortest of the U-shaped tracts *(23).* We speculate that this anatomical shortcut can contribute to the rapid learning and perceptual enhancement of social associations (e.g., the shape and the badge used here).

Our evidence for changes in IA-IFG connectivity was confined to the left hemisphere. Evidence for left-hemisphere dominance in perceptual matching to social stimuli has been observed before (*15*). While previous studies have used shape-label matching, here we employed non-verbal stimuli making it less likely that the left hemisphere dominance arose due to verbal labels being used. A different account can be formulated from the proposal made by Craig *(24)* that the left hemisphere mediates group-oriented affiliative emotions.

We also found that functional connectivity between the AI and the DLPFC decreased after the task was performed compared to prior to the task. This finding might imply that throughout the task participants’ responses became more automatic and therefore task performance did not require as much attentional control as required to start with. Previous studies relate the functional coupling between AI and DLPFC to memory retrieval *(25)*, which is consistent with our interpretation of the development of automaticity in the retrieval of shape-badge associations and with reduced effort being required as practice increased. The positive versus negative functional connectivity between the AI and (i) the IFG and (ii) the DLPFC respectively can also be explained in relation to attention *(26).* Recent models of attention posit that the AI and IFG work as a part of cingulo-opercular attention system which helps maintain attention throughout a task. In contrast the DLPFC operates as a part of a fronto-parietal attention system, which plays a role in rapid adaptive control *(26).* Note that the need for rapid adaptive control may decrease as a task becomes more automated.

In conclusion, the increased connectivity we found in this study between the left AI and IFG suggests these areas are functionally coupled in order to respond to socially salient stimuli, even in simple perceptual matching tasks, and that there is rapid modulation of neural connectivity between these regions through new learning of in- and out-group associations. We conclude that alterations in resting state AI-IFG connectivity may be the underlying neural substrate of learned in-group bias.

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**Supplementary materials**

**Materials and Methods**

Figs. S1 to S8

Table S1, S2

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**Figure 1.** Example activation map related to task performance vs. rest (N=20).

**Figure 2.** Statistical map of the intrinsic connectivity between the seeds of interest (a) Pre-task random effect functional connectivity analyses (Bonferroni corrected, *p<.01*). (b) Post-task random effect functional connectivity analyses (Bonferroni, *p<.01*). (c) Altered functional connectivity in post-task compared to the pre-task (uncorrected, *p<.05*).

**Figure 3.** Positive correlation between the strength of the post-task functional connectivity for AI/ IFG pair and the size of in-group bias based on the RT difference for in- vs. out-group stimuli.

**Figure 4.** Positive correlation between the changes in the strength of functional connectivity in post- versus pre-task for AI/ IFG pair and the size of in-group bias based on the RT difference for in- vs. out-group stimuli.