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**Neural Mechanisms of Resistance to Peer Influence  
in Early Adolescence**

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## **Abstract**

During the shift from a parent-dependent child to a fully autonomous adult, peers take on a significant role in shaping the adolescent's behaviour. Peer-derived influences are not always positive, however. Here we explore neural correlates of inter-individual differences in the probability of resisting peer influence in early adolescence. Using functional magnetic-resonance imaging (fMRI), we found striking differences between 10-year old children with high and low resistance to peer influence in their brain activity during observation of angry hand-movements and angry facial expressions: compared with subjects with low resistance to peer influence, individuals with high resistance showed a highly coordinated brain activity in neural systems underlying perception of action and decision making. These findings suggest that the probability of resisting peer influence depends on neural interactions during observation of emotion-laden actions.

Keywords: Adolescence; Peer-Influence; fMRI; Action Observation; Prefrontal Cortex;

## **Introduction**

At the onset of adolescence, several key processes engaged during social interactions, such as face processing (Taylor et al., 1999), emotion recognition (Batty and Taylor, 2006) or perspective taking (Choudhury and Blakemore, 2006), are still immature. Given the amount of time adolescents spend with their peers, it is not surprising that peers are influential in modelling the adolescent emotional and social cognitive abilities (Steinberg and Silverberg, 1986; Steinberg, 2005). To date, little is known about the neural bases of social interactions during adolescence, despite a growing body of research on the structural and functional maturation of the adolescent brain (Paus, 2005; Blakemore and Choudhury, 2006). In particular, we do not know how inter-individual differences in the susceptibility to social influences, such as peer pressure, might be linked to differential neural processing of socially relevant stimuli.

Here we explore the relationship between the capacity to resist peer influence in early adolescence and brain activity during perception of face or hand movements performed with an emotion.

Human and non-human primates engage a number of cortical regions when observing con-specifics (“actors”). Two neural systems stand out: (1) regions in the temporal cortex involved in the processing of biological motion (Allison et al., 2000); and (2) fronto-parietal regions involved in programming and executing motor actions (Rizzolatti and Craighero, 2004). The former extract information from visual cues embedded in the actor’s movements, whereas the latter may support computations used to infer the actor’s

intentions and/or to facilitate initiation, by the observer, of actions matching those of the actor.

To investigate possible links between the sensitivity to peers' actions and the recruitment of these neural systems during the observation of others, we scanned early adolescents while they watched video-clips of hand or face movements. Those movements were performed either in a neutral way or with anger. We chose anger because it is the basic emotion that is best recognized from goal-directed (non-communicative) hand actions (Pollick et al., 2001). Furthermore, perception of anger, and thereby of potential threat, is essential for social interactions. The analysis of fMRI data focused on the variations in both local and inter-regional patterns of brain activity as a function of resistance to peer influence (RPI). RPI was assessed with a self-report questionnaire for adolescents designed to minimize socially desirable responding (see Appendix). This instrument has been used in a number of large sample studies. Scores stay low during early adolescence and increase linearly from 14 years of age to reach adult levels at 18; this pattern is consistent across ethnic groups, reflecting the reliability and generalization of the measure (Steinberg 2006). In a population of serious juvenile offenders, we found that the presence of antisocial peers in one's network predicts one's own criminal behaviour to a significantly greater extent in individuals with low RPI scores than among those who have equally antisocial peers but score high on RPI (Monahan et al. 2007). This finding confirms construct validity of the RPI measure and its predictive value in evaluating inter-individual differences in peer relationships.

## **Procedures and Methods**

*Subjects.* Forty six typically developing children (age: 10 yr  $\pm$  4.4 months, age range: 9.4 to 10.8 years, 24 boys and 22 girls) participated in the study which involved a questionnaire and a series of behavioural tests, including the Stroop test, a self-order pointing task (Petrides and Milner, 1982) and the Wechsler Intelligence Scale for Children (WISC-III) test battery, as well as an fMRI session. All participants filled out the Puberty Development Scale (PDS; Peterson et al., 1988), which is an eight-item self-report measure of physical development based on the Tanner stages with separate forms for males and females. For this scale, there are five categories of pubertal status: (1) prepubertal, (2) beginning pubertal, (3) midpubertal, (4) advanced pubertal, (5) postpubertal. The mean ( $\pm$ Standard Deviation) of the Tanner stages were 1.4  $\pm$  0.7 (boys) and 2.2  $\pm$  1.0 (girls).

*Questionnaire.* The Resistance to Peer Influence (RPI) questionnaire (Steinberg, 2006) consists of 10 pairs of opposite statements about inter-individual interactions, such as “Some people hide their true opinion from their friends if they think their friends will make fun of them because of it” and “Other people will say their true opinion in front of their friends, even if they know their friends will make fun of them because of it”. The participant has to indicate which one is more like her or him and to what degree (“sort of true of me” or “really true of me”) he/she identifies with the statement. The scoring is such that a high score on a one-to-four scale indicates a high resistance to peer influence, whereas a low score indicates a great susceptibility to peer influence. This questionnaire has been tested in four large samples (700 to 1350 individuals) from different populations for which inter-questions reliability

(Cronbach's alpha) have proven adequate and highly similar (Steinberg 2006). These include: (1) A predominantly impoverished and ethnic minority sample of 1,350 serious juvenile offenders in two U.S. cities, ages 14-18 years (alpha = .73); (2) A sample of approximately 700 individuals aged 11-24 yr in juvenile detention or jail, from four U.S. cities (alpha = .76); (3) A predominantly poor and working-class sample of 700 individuals in the community in four U.S. cities living in the same neighborhoods as participants in Sample 2 (alpha = .70); and (4) A multi-ethnic working and middle class community sample of 935 individuals aged 10-30 yr, from five US regions (alpha = .74).

*Functional MRI.* We acquired fMRI datasets while children watched short videoclips of hand actions and facial expressions; the subjects had no other task while watching the videoclips. The stimuli and experimental protocol were identical to those used previously in young adult subjects (Grosbras and Paus, 2006). Stimuli were presented in 18-sec blocks. Hand actions consisted of reaching, grasping and manipulating eight different objects (phone, pencil, spoon, computer mouse, glass, hammer, screwdriver, and cup) in either a neutral or an angry way (in separate blocks). Movements performed with anger differed from neutral movements in their acceleration profile but both types of movements were matched for the mean duration of the reaching phase, as well as for the hand-object interaction. Angry face stimuli consisted of male or female faces starting from a neutral expression and moving to express anger. Neutral faces stimuli were extracted from periods of video recordings when the actors were not expressing any emotion but were nonetheless moving their face (e.g. twitching their nose, opening their mouth,

blinking their eyes). The control stimuli consisted of black-and-white concentric circles of various contrasts, expanding and contracting at various speeds, roughly matching the contrast and motion characteristics of the faces and hands clips. Scanning was performed on a 1.5 Tesla Siemens Sonata scanner. First, we acquired a high resolution T1-weighted 3D structural image (matrix 256x256x170; 1mm<sup>3</sup> voxels) for anatomical localization and co-registration with the functional time-series. A series of blood oxygen-level dependent (BOLD) T2\*-weighted gradient-echo, echo-planar images was then acquired (matrix size 64x64; TE = 50 ms; TR = 3secs; 180 32-slice frames collected after the gradients had reached steady-state, voxel size 4x4x4 mm<sup>3</sup>). The images were assessed for head motion and realigned to the first frame using AFNI (Cox, 1996). Then they were spatially smoothed using a 6-mm full-width-half-maximum Gaussian filter. We checked that motion did not exceed one millimeter or one degree in any direction. This was not the case in 11 out of 46 children and these subjects were excluded from the subsequent analyses; the final sample consists of 35 children (age: 10 yr ± 4.5 months, age range: 9.4 to 10.7 years, 20 boys and 15 girls).

*Correlation analysis.* First we assessed, for each voxel, the differences in BOLD signal induced by neutral or emotional hand or face movements and the non-biological movements baseline condition; this analysis was carried out using the general linear model as implemented in the fmristat Matlab (Mathworks) toolbox (Worsley et al., 2002). Then we computed, voxel-by-voxel, the correlation between these differences and scores obtained for the RPI questionnaire. The threshold for  $p < 0.05$  corrected for multiple comparisons was determined using a method based on local discrete



maxima, which was the most accurate for the effective smoothness of the data (Worsley, 2005). This analysis allows us to identify brain regions, engaged during the passive observation of others' movements, where the variations in BOLD signal are related to RPI scores.

*Partial least square analysis.* Second, we analyzed the fMRI datasets with a multivariate technique, partial least squares (PLS), with the aim of extracting coordinated patterns of brain activity influenced by resistance to peer influence (McIntosh and Lobaugh, 2004). For each of the five experimental conditions, namely Neutral Hand Actions, Angry Hand Actions, Neutral Facial Expressions, Angry Facial Expressions and Non-biological Visual Motion, we computed the correlation between each voxel's time series during this condition and the score each subject obtained with the RPI questionnaire. These correlation matrices are put into one large matrix and subjected to singular value decomposition. This produces orthogonal latent variables (LV), each consisting of a behavioral LV and a brain LV, as well as a singular value, which indicates the strength of the covariance between the pattern of brain activity and the questionnaire score. The brain LV identifies a pattern of voxels that, as a whole, show covariation between fMRI signal and behavior. The behavioral LV contains weights for the correlation images obtained for the five different conditions, therefore representing how much each condition contributes to the brain LV. This allows us to produce maps of similarities or differences in brain-behavior correlations between conditions. The significance of each pair of behavioral and brain LV is assessed by a permutation test: 500 matrices are created shuffling the condition labels at each time point and then subjected to decomposition. Exact statistics are

derived assessing how often a singular value higher than the one derived from the data could be observed by chance. Then, to estimate the reliability of the spatial pattern identified by an LV, 100 bootstrap samples were used to identify those voxels whose correlation with behavior is the most robust.

To visualize the pattern on inter-regional correlations, we have generated an inter-regional correlation matrix for the Angry Hand Actions, a condition identified by the PLS as distinguishing the low from high RPI subjects (see below). We have done so separately for the subjects with high and low resistance to peer influence (i.e. above or below the median). The High RPI group consisted of 6 girls (Mean $\pm$ SD; 10.1 $\pm$ 0.37 years, 1.8 $\pm$ 1.1 Tanner stage) and 11 boys (10 $\pm$ 0.36 yr, 1.2 $\pm$ 0.4 Tanner stage), and the Low RPI group consisted of 9 girls (10 $\pm$ 0.4 yr, 2.4 $\pm$ 1 Tanner stage) and 9 boys (10 $\pm$ 0.4 yr, 1.8 $\pm$ 0.8 Tanner stage).

## **Results**

The average score in the RPI questionnaire for the 35 subjects included in the analysis was 2.88 (standard deviation 0.44, median 2.84).

Using the standard univariate analysis based on the general linear model (GLM), we found similar BOLD response to hand (neutral, angry) and face (neutral, angry) stimuli as observed in adults previously (Grosbras and Paus 2006). A summary of these results is provided in Supplementary Table 2. In short, the observation of hand movements engaged fronto-parietal and middle temporal regions. Angry hand movements also recruited part of the parietal operculum/supramarginal gyrus, the medial prefrontal cortex, and the amygdala. The observation of angry or neutral faces engaged the premotor

cortex, various parts of inferior and medial frontal cortex the fusiform cortex, the superior temporal sulcus and the amygdala.

*Correlation analysis* Using univariate GLM-based analysis, we detected a negative correlation between the RPI scores and the increase in BOLD signal, as compared with the baseline, during the observation of angry (but not emotionally neutral) hand or face movements, in the right dorsal premotor cortex (MNI152 coordinates  $x=40$   $y=8$   $z=44$ ). Thus, children with lower resistance to peer influence had higher BOLD response to angry movements in this region than children with higher resistance. Moreover, the RPI scores correlated negatively with the increase in BOLD signal in the left mid-dorsolateral prefrontal cortex ( $x=-52$   $y=36$   $z=28$ ) during the observation of angry hand (but not face) movements. This latter region, together with the right intraparietal sulcus ( $x=36$   $y=-40$   $z=60$ ), the left frontal eye field ( $x=-24$   $y=-16$   $z=51$ ) and anterior cingulate cortex ( $x=4$   $y=12$   $z=44$ ) also showed a correlation between RPI scores and the BOLD response measured in the direct contrast between angry and neutral hand movements when the threshold was set at  $p<0.001$ , uncorrected for multiple comparisons.

*Partial least square analysis.* Multivariate PLS-based analysis revealed two significant ( $p<0.05$ ; 500 permutations, 100 bootstraps) latent variables (LV): (1) LV1 ( $p<0.006$ ) explained 29% of the covariance between the fMRI data and the RPI scores and showed a strong positive correlation ( $r=0.68$ ) between the scores and fMRI signal measured during the observation of angry hand actions; and (2) LV2 ( $p<0.034$ ) explained 20% of the covariance and indicated

a strong negative ( $r=-0.94$ ) correlation between RPI scores and fMRI signal measured during the observation of angry facial expressions. Note that this pattern of coordinated brain activity differentiating children more or less able to resist peer influence was found only when they watched emotion-laden videoclips. Figure 1 illustrates these findings and Supplementary Table 1 contains a list of brain regions identified by LV1 and LV2. Three features stand out here. First, many of these regions are part of the two neural systems outlined in the introduction, namely the temporal regions involved in the processing of biological motion and fronto-parietal regions involved in the programming and execution of movement. But LV1 also identified a set of prefrontal regions that are involved in various aspects of executive functions and decision-making. Second, the degree of inter-regional correlations (i.e. functional connectivity) is higher in children with high- vs. low resistance to peer influence (see Figure 1 d-e); the two groups differed significantly in the mean pair-wise correlation coefficients calculated across all 26 regions ( $F_{1,649}=72.6$ ,  $p<0.0001$ ). Third, the above pattern of coordinated brain activity differentiating children more or less able to resist peer influence is found only when they watched videoclips of hand actions performed with anger; no such relationships were observed for the remaining experimental conditions.

*Other behavioral measures.* Would children with high resistance to peer-influence differ from those with low resistance if asked explicitly to perform “executive” tasks? We found significant differences between the two groups in the number of corrected errors made during the Stroop test of interference in language domain ( $F=8.04$ ,  $p<0.01$ ), and in the number of errors in the Self-

ordered Pointing test of working memory ( $F=8.2$ ,  $p<0.01$ ); both results suggest better self-monitoring abilities of children with high resistance to peer influence. The two groups did not differ significantly in their general intelligence, as assessed by the Wechsler Intelligence Scale for Children (WISC-III; Low RPI:  $117\pm 9$  ( $M\pm SD$ ) High RPI:  $113\pm 12$ ).

## **Discussion**

### *Correlation between frontal cortex activity and peer-influence resistance*

We observe a correlation between the sensitivity to peer influence and the engagement of two frontal regions, the right dorsal premotor cortex and the left dorsolateral prefrontal cortex, while the children watched angry hand actions or face movements. The dorsal (unlike ventral) premotor cortex is not very often reported in studies of action observation. Its recruitment might reflect the automatic engagement of the motor preparation system when we observe an action performed with someone else or even just the outcome of this action (Cisek and Kalaska, 2004; Grosbras and Paus, 2006). Therefore it is possible that motor preparation induced by angry movement will be more solicited in children more sensitive to peer pressure. The dorsolateral prefrontal cortex is involved in attentional control and inhibition of prepotent responses. Its activity during attentional tasks, in particular antisaccades, changes during adolescence together with the activity in other part of the attentional network such as frontal eye field and anterior cingulate cortex (Luna et al., 2001). More sensitive children might engage more attentional resources when presented with salient stimuli such as angry hand movements.

*Differences in functional connectivity in relation to peer-influence resistance.*

The PLS analysis allowed us to go one step further and to observe that a degree of functional connectivity across a set of cortical regions predicts resistance to peer influence. In this context, the most significant prediction emerged when subjects watched angry hand actions. The pattern of inter-regional correlations identified by this method includes both (i) regions involved in action observation: from the fronto-parietal as well as from temporo-occipital system discussed in the introduction and (ii) regions in the prefrontal cortex. The most striking finding is that the functional connectivity between these regions during a passive task differentiates children with high or low resistance to peer influence. The children simply watched the videoclips as they would watch their peers in a situation where no clear goals have been formulated in advance. And yet, a number of prefrontal regions showed coordinated changes in the fMRI signal that correlated with those in the other two neural systems involved in action observation. Typically, prefrontal cortex is engaged when the subject performs an explicit task requiring, for example, manipulation of information in working memory, inhibition of prepotent responses and/or suppression of interference, or planning and decision-making (Petrides, 2005). No such demands were explicitly made in this study. It is important to note the difference between the findings obtained with univariate and multivariate analyses here. Univariate, voxel-by-voxel, correlation between the fMRI signal and RPI scores showed a more robust response in low-resistance children independently in the

premotor cortex and the prefrontal cortex. The multivariate analysis, on the other hand, revealed stronger inter-regional correlations, or functional connectivity, between these and other regions in high-resistance children. We speculate that these two phenomena reflect, respectively, higher sensitivity of low-resistance children to socially relevant input and higher inter-regional integration of such inputs in high-resistance children. It is possible that the brains of the children with high resistance to peer influence engage *automatically* “executive” processes when challenged with relatively complex and socially relevant stimuli. Interestingly the children with higher resistance to peer influence were also those who performed better in (explicit) executive tasks.

#### *Generalisation to other emotions*

The brain-behavior correlations were observed when children observed movements performed with anger, but not for neutral movements. Emotionally neutral movements of peers, although socially relevant, might not require as much processing resources as angry movements. One can easily imagine that interacting, or avoiding an interaction, with a peer displaying anger, and thereby a potential threat, will require additional self-control over one’s behavior. Our results show that “low-resistance” (“peer sensitive”) children present a more robust fMRI response to anger during action observation, as compared with “high-resistance” children. Our data also indicate that children who are more able to resist peer influence show also a more coordinated brain activity during the processing of anger. Our results do not, however, allow us to tease apart whether these differences are especially linked to the

observation of anger or could be due to the efficient processing of any other strong emotion. Future studies should investigate whether resistance to peer influence also determines brain coordination during the processing of other basic or complex emotions that are more (e.g. trustworthiness) or less (e.g. surprise) related to peer interactions.

#### *Resistance to Peer Influence and other behavioral characteristics*

Individuals with high and low RPI scores are likely to differ in a number of cognitive and behavioral characteristics. In our sample, for example, they differed in the number of *corrected errors* in the Stroop test. In analyses of questionnaire-based data from the MacArthur Juvenile Culpability Study (Steinberg et al., 2007) we observed that, after controlling for age, RPI scores were significantly, albeit very modestly, negatively correlated with widely used measures of impulsivity (the Barratt Impulsiveness Scale; Patton et al. Barratt, 1995) and antisocial risk-taking (the Benthin Risk Perception Measure; Benthin et al, 1993). In analyses of data from the Pathways to Desistance Study (Schubert et al., 2004), RPI scores were significantly positively correlated with a measure of Impulse Control (from the Weinberger Adjustment Inventory; Weinberger and Schwartz, 1990) and significantly negatively correlated with responses to the item, “I worry what others think of me,” from the Revised Children’s Manifest Anxiety Scale (Reynolds and Richmond, 1985). Taken together, it appears that individuals with high vs. low RPI scores may be characterized by better abilities required to control impulsive behavior in social context. Further work is required to dissect these behavioral traits on cognitive level in different adolescent populations.



### *Conclusion*

Overall, our results suggest that enhanced neural interactions across brain regions involved in processing non-verbal socially relevant cues, planning, programming and executing motor behaviour underlie, at least in part, resistance to peer influence in early adolescence. These findings provide the first step towards exploring the neural factors that may make children and adolescents more sensitive to peer influence. They also offer insights that may inspire the development of strategies aimed at enhancing resistance to peer pressure (Donaldson et al., 1995) such that the adolescent can maintain his/her autonomy in a group of peers. Further studies are required to examine this relationship throughout adolescence in order to evaluate the effects of age, sex and sexual maturation.

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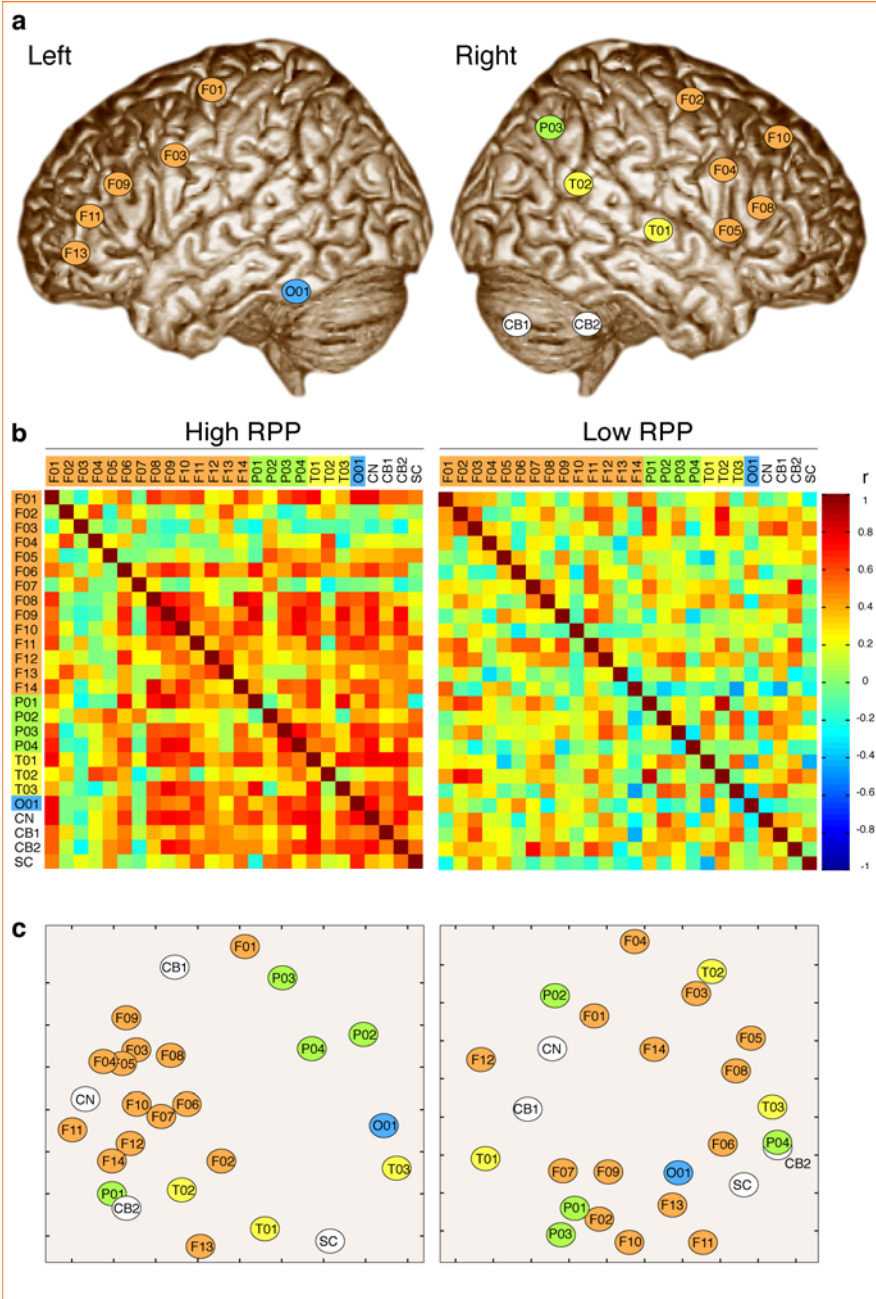
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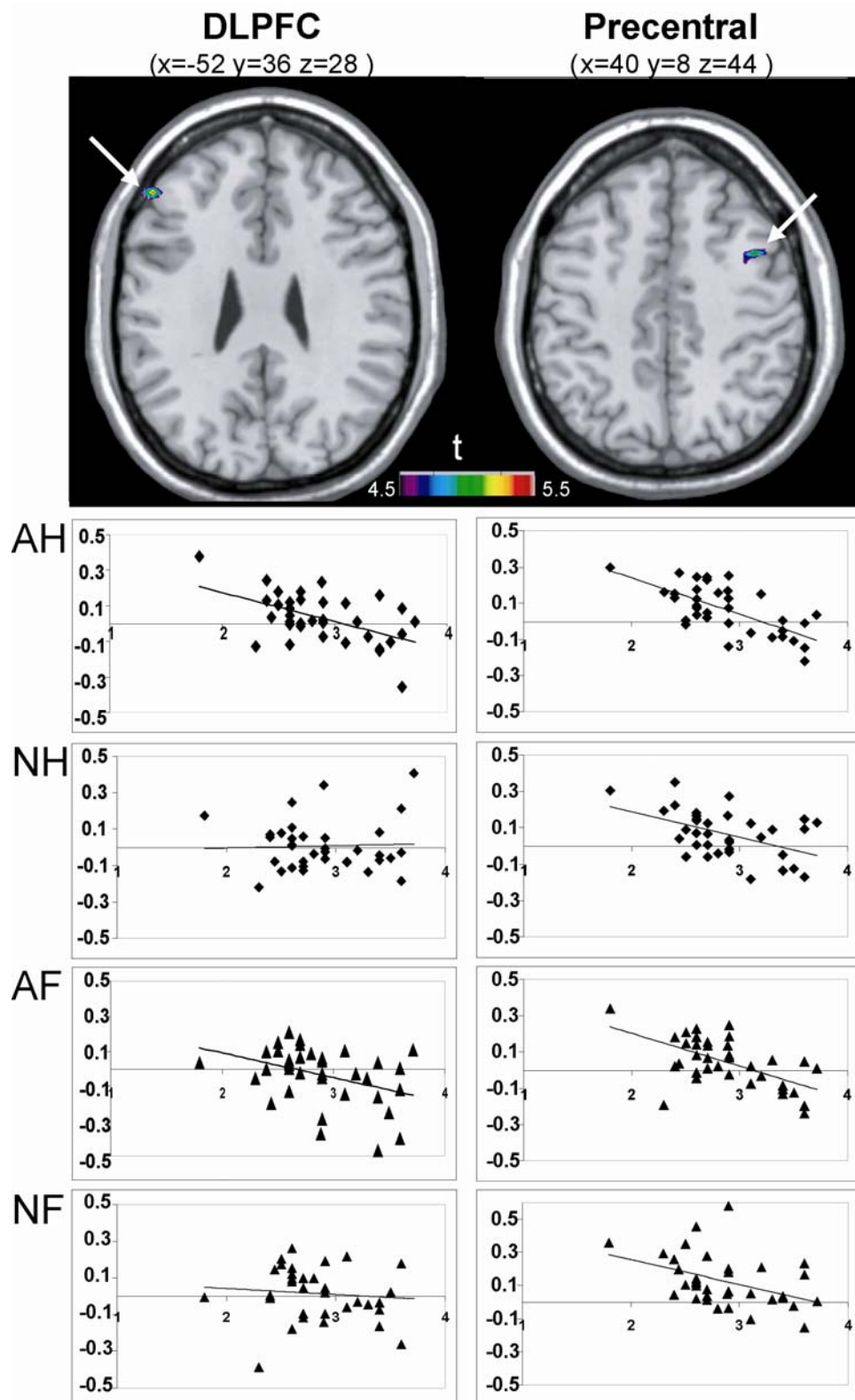
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**Figure 1.** Inter-regional correlations in fMRI signal during the observation of angry hand movements. **a**, Latent Variable 1 (LV1) identified a combination of brain regions that, as a whole, correlated with the Resistance-to-Peer-Influence (RPI) scores. Note that high correlations are observed only for fMRI signal measured during the observation of Angry Hand Movements. **b**, Brains scores (weighted sum of all voxels in an image for each subject, using the weights derived from the brain LV1) derived from the fMRI signal measured during Angry Hand Movements plotted as a function of RPI. **c**, Locations of brain regions identified by LV1; only regions visible on the lateral surface of the left and right hemispheres are shown. **d**, Correlation matrices depicting inter-regional correlations of fMRI signal measured during the observation of Angry Hand Movements, as revealed by LV1, in subjects with High (left) and Low (right) Resistance to Peer Influence. The High and Low RPI subgroups correspond to the subjects with RPI scores above and below the group median, respectively. The region labels match those included in Supplementary Table 1. **e**, Multidimensional scaling (MDS) representations of the inter-regional correlations of the 26-D matrix depicted above; in the MDS 2-D plots, strongly correlated regions are placed close together. Note, for example, the close grouping of premotor (F03 and F04) and prefrontal (F08 and F09) fronto-cortical regions. The region labels match those included in Table 1. **F01**, Premotor cortex, dorsal, left; **F02**, Premotor cortex, dorsal, right; **F03**, Premotor cortex, ventral, left; **F04**, Premotor cortex, ventral, right; **F05**, Frontal operculum, right; **F06**, Cingulate motor area, left; **F07** Insula, anterior, left; **F08**, Prefrontal cortex, ventro-lateral, right; **F09**, Prefrontal cortex, dorso-lateral, left; **F10**, Prefrontal cortex, dorso-lateral, right; **F11**, Prefrontal cortex,

ventro-lateral, left; **F12**, Anterior cingulate cortex, right; **F13**, Orbito-frontal cortex, lateral, left; **F14**, Prefrontal cortex, medial; **P01**, Posterior cingulate cortex; **P02**, Precuneus, left; **P03**, Parietal cortex, dorso-lateral, right; **P04**, Parietal cortex, dorso-medial, right; **T01**, Superior Temporal Sulcus, middle, right; **T02**, Superior Temporal Sulcus, posterior, right; **T03**, Hippocampus, right; **O01**, Fusiform gyrus, left; **CN**, Caudate nucleus, right; **CB1**, Cerebellum, right; **CB2**, Cerebellum, right; **SC**, Superior Colliculus, right.







Supplementary Figure 1. The top two images show the cortical regions in which the change of fMRI signal (Angry Hand condition minus Control) correlated significantly with RPI scores ( $p < 0.05$  corrected for multiple comparisons). The eight lower panels show plots of the change in fMRI signal (arbitrary units since proportional scaling was applied) against the RPI scores obtained in the 35 subjects included in the analysis. Red asterisks identify significant correlations. DLPFC, Dorsolateral Prefrontal Cortex; Premotor, dorsal premotor cortex; AH, Angry Hand condition; NH, Neutral Hand condition; AF, Angry Face condition; NF, Neutral Face condition.