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Wi Hoon Jung

Kristin Prehn

Zhuo Fang

Marc Korczykowski

Joseph W. Kable
University of Pennsylvania

See next page for additional authors

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Abstract

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Keywords

moral competence, individual differences, functional connectivity, resting-state fMRI, amygdala

Disciplines

Biological Psychology | Business Law, Public Responsibility, and Ethics | Law | Legal Studies | Neuroscience and Neurobiology

Author(s)

Wi Hoon Jung, Kristin Prehn, Zhuo Fang, Marc Korczykowski, Joseph W. Kable, Hengyi Rao, and Diana C. Robertson

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Moral competence and brain connectivity: a resting-state fMRI study

Wi Hoon Jung[1], **Kristin Prehn**[2], **Zhuo Fang**[3,4], **Marc Korczykowski**[3,5], **Joseph W. Kable**[1], **Hengyi Rao**[3,4,*], and **Diana C. Robertson**[5,*]

[1]Department of Psychology, University of Pennsylvania, Philadelphia, United States of America

[2]Department of Neurology & NeuroCure Clinical Research Center, Charité Universitätsmedizin Berlin, Germany

[3]Center for Functional Neuroimaging, Department of Neurology, University of Pennsylvania, Philadelphia, United States of America

[4]Laboratory of Applied Brain and Cognitive Sciences, Shanghai International Studies University, Shanghai, China

[5]Department of Legal Studies & Business Ethics, The Wharton School, University of Pennsylvania, Philadelphia, United States of America

Abstract

Moral competence (MC) refers to the ability to apply certain moral orientations in a consistent and differentiated manner when judging moral issues. People greatly differ in terms of MC, however, little is known about how these differences are implemented in the brain. To investigate this question, we used functional magnetic resonance imaging and examined resting-state functional connectivity (RSFC) in n=31 individuals with MC scores in the highest 15% of the population and n=33 individuals with MC scores in the lowest 15%, selected from a large sample of 730 Master of Business Administration (MBA) students. Compared to individuals with lower MC, individuals with higher MC showed greater amygdala-ventromedial prefrontal connectivity, which may reflect better ability to cope with emotional conflicts elicited by moral dilemmas. Moreover, individuals with higher MC showed less inter-network connectivity between the amygdalar and fronto-parietal networks, suggesting a more independent operation of these networks. Our findings provide novel insights into how individual differences in moral judgment are associated with RSFC in brain circuits related to emotion processing and cognitive control.

*Correspondence should be addressed to: Hengyi Rao, PhD, Center for Functional Neuroimaging, Department of Neurology, University of Pennsylvania, 3W Gates, 3400 Spruce Street, Philadelphia, PA 19104, USA, Phone: (01)215-746-2470, hengyi@mail.med.upenn.edu Or Diana Robertson, PhD, Department of Legal Studies & Business Ethics, The Wharton School, University of Pennsylvania, 671 Huntsman Hall, 3730 Walnut Street, Philadelphia, PA, 19104, USA, Phone: (01)215-898-5919, robertsd@wharton.upenn.edu.

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Keywords

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1. Introduction

Human beings, unlike other animals, are able to make judgments of right and wrong about their own and others' actions according to norms and values established in a society. This ability is termed "moral judgment" or "moral decision-making." As people vary in the development of their cognitive abilities, people also vary in the development of the ability to solve more complex social (moral) problems. Individual differences in moral judgment can be captured by evaluating the level of moral development based on Kohlberg's theory (Kohlberg, 1984). He proposed that people progress in their ability to judge moral issues through a series of six stages that can be arranged into three levels as cognitive abilities mature: pre-conventional (to judge moral issues based on personal interests), conventional (to judge based on social norms), and post-conventional levels (to judge based on universal ethical principles). Each level is grounded on specific cognitive schemas that can be objectively assessed by the Defining Issues Test (DIT-2) developed by Rest and colleagues (1999). Another and complementary approach to investigate individual differences in moral judgment is to evaluate the ability to use the arguments of a particular moral level consistently when judging moral issues. Lind (2008) proposed the Dual Aspect Theory in which morality is defined as consisting of two distinct yet inseparable aspects: preferences for certain moral orientations (affect aspect) and the ability to consistently judge according to these preferences (cognitive aspect). The latter aspect is called moral competence (MC) and can be measured with the Moral Competence Test (MCT, formerly called Moral Judgment Test, MJT).

Many functional magnetic resonance imaging (fMRI) studies across a variety of different moral reasoning tasks show a remarkably consistent pattern of activation, particularly in brain regions involved in cognitive and emotional processes. These brain regions include the ventromedial prefrontal cortex (vmPFC), medial frontal cortex, and posterior cingulate cortex, which are considered part of the default mode network (Greene et al., 2001; Buckner and Carroll, 2006), as well as the temporal poles, posterior superior temporal sulcus (pSTS), amygdala, dorsolateral prefrontal cortex (DLPFC), and parietal lobe (Greene and Haidt, 2002; Moll et al., 2005; Prehn and Heekeren, 2009).Moreover, neuroimaging and clinical studies provide convergent evidence that cognitive and emotional processes both compete (Greene and Haidt, 2002; Koenigs et al., 2007) and cooperate with each other during moral decision-making (Moll and de Oliverira-Souza, 2007; Moll et al., 2008). Thus, researchers have suggested that an individual's ability to intelligently use emotional and cognitive processes, sensitive to the context of the specific moral situationfaced, is key to decision-making, emphasizing the role of individual differences in emotional and cognitive information processing (Prehn and Heekeren, 2009; 2014; Talmi and Frith, 2007).

As mentioned above, MC is the ability to apply certain moral orientations in a consistent and differentiated manner in varying social situations. Thus, social norms and values represented

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as affectively laden moral orientations are linked by means of MC with everyday behavior and decision-making (Prehn and Heekeren, 2009). In other words, while the level of moral reasoning describes a person's moral orientations and principles, MC refers to the ability to consistently apply these moral norms and principles. For a consistent application of moral norms and principles it might be helpful to regulate emotion elicited by a moral dilemma. Indeed, it has been suggested that emotion regulation plays an important role in moral judgments (Hu and Jiang, 2014; Szekely and Miu, 2015a). With reduced emotional responses or less emotional interference people might be better able to reason and to apply moral norms and principles. Taken together, investigating the neural mechanisms of MC may provide important clues about the neural basis of individual differences in the intelligent use of the cognitive and emotional processes on moral dilemmas. However, little is known about the neural basis underlying individual differences in MC. To date, only one study so far has explicitly investigated neural mechanisms associated with individual differences in MC and reported greater activity in the DLPFC, vmPFC, and pSTS in individuals with lower MC during a moral judgment task (Prehn et al., 2008).

Functional connectivity (FC) refers to the functional integration of brain areas as the result of neuronal interactions, which is measured by the temporal correlations of neural activity in remote brain regions (Friston, 1994). Particularly, resting-state fMRI (RS-fMRI) has recently emerged as a useful tool to understand the FC of the brain (Biswal et al., 1995; Fox and Raichle 2007). Previous studies reported strong resemblances between the spatial patterns of resting-state FC (RSFC) maps, called resting-state networks (RSNs), and spatial activity patterns observed during demanding tasks, including the motor, language, default mode, and fronto-parietal control networks (FPCN, Biswal et al., 1995; Fox et al**.,** 2005; Jung et al., 2012; Buckner et al., 2013). Importantly, recent studies demonstrated that the strength of RSFC within certain networks is associated with affect and emotional processing (van Marle et al., 2010) and cognitive abilities such as working memory and reading performance (Hampson et al., 2006; Zhang et al., 2014).Moreover, studies revealed that the strength of FC between particular RSNs, so-called inter-network connectivity, is associated with cognitive performance such as working memory and executive function (Hampson et al., 2010; Repovs et al., 2011),as well as psychiatric patients' clinical symptoms (Mamah et al., 2013; Repovs et al., 2011). Thus, investigating FC of key regions related to cognitive and emotional processing and interactions between these networksmay provide insight into the neural mechanisms involved in moral judgment. Here, we investigated how individual differences in MC are reflected in intrinsic functional architecture using RSFC analyses. To do this, we carefully selected our sample in terms of high and low MC scores to compare the strengths of RSFC between individuals at the extremes of MC, rather than examining correlations between RSFC and MC scores across the entire spectrum. Particularly, we focused on the amygdalar network involved in emotion processing and regulation and the FPCN involved in goal-directed cognition, based on recent studies showing the functional contribution of these regions to emotional and cognitive processing in moral judgment (Shenhav and Greene, 2014; Greene, 2014). First, we applied a seed-based FC approach to test whether the amygdala and DLPFC/parietal lobe were differentially connected to other brain regions in the two groups. Second, we defined nodes in the amygdalar network and FPCN based on previous studies and applied a region of interest (ROI)-based inter-network

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FC approach to test group differences in FC between these two networks across the two groups. Previous studies have reported that the strength of FC between amygdala and vmPFC varies to the extent to which emotional input is integrated with cognitive processes during moral dilemmas (Shenhav and Greene, 2014) and that individuals with psychopathic traits, characterized by moral insensitivity, had less FC between amygdala and orbitofrontal cortex (OFC) adjacent to vmPFC (Marsh et al., 2011). Additionally, further studies reported an increase in inter-network connectivity between the amygdalar network and FPCN in clinical patients characterized by deficits in emotion regulation (Etkin et al., 2009; Lois et al., 2014). As explained above, emotional-cognitive integration (i.e., moral sensitivity) and the ability to regulate emotions elicited by a moral situation might be necessary to consistently apply moral norms and principles (i.e., for moral competence). Therefore, based on previous literature, we hypothesized that compared to individuals with lower MC, individuals with higher MC have increased amygdala-vmPFC coupling and reduced inter-network connectivity between the amygdalar network and FPCN.

2. Materials and Methods

2.1. Participants

We enrolled a total of 730 Master of Business Administration (MBA) students (mean age 27.1 years, range 24–33 years). This sampling approach was intended to result in a relatively homogenous group with respect to level of educational experience, because educationmay affectboth MC and moral development levels (Lind, 2008; Rest and Thoma, 1985). The entire sample first took an online version of the Moral Competence Test (MCT; Lind and Wakenhut, 1980) to measure MC. Then, according to their MCT C-scores, two subsets of students (n=67) who scored above 85% (i.e., high C-score group, HCSG, n=33) and below 15% (i.e., low C-score group, LCSG, n=34) were selected, and asked to participate in the MRI part of the study. Of note, T1-weighted anatomical data from this dataset were already reported elsewhere (Prehn et al,. 2015). From this dataset, the RS-fMRI data of three participants (2 HCSG and 1 LCSG) were excluded because of excessive head motion defined as (i) >3 mm translation or >3° of rotation and (ii) mean framewise displacement >0.5mm (Power et al., 2012) to reduce the effect of head motion on FC maps. Thus, a total of 64 participants were included in the final analyses (see Table 1).

All individuals provided informed written consent before participation. This study was approved by the Institutional Review Board of the University of Pennsylvania.

2.2. Moral competence

We used the Moral Competence Test (MCT; Lind, 1982, 2008) to assess individual variation in MC. The MCT asked a participant to assess two moral dilemmas: the workers dilemma and the doctor dilemma. In the doctor dilemma, for example, a woman had cancer with no hope for being cured. She suffered terrible pain and begged the doctor to aid her in committing medically assisted suicide (by giving her an overdose of morphine) because she could no longer endure the pain and would be dead in a few weeks anyway. The doctor complied with her wish. After presentation of this short story, the participant is first asked to judge whether the protagonist's solution was right or wrong on a seven-point Likert scale,

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and then asked to rate six arguments supporting (pro-arguments) and six arguments rejecting (counter-arguments) the protagonist's solution in terms of its acceptability on a nine-point Likert scale. Each argument represents a certain moral orientation (according to the six Kohlbergian stages; Kohlberg, 1984).An example for a low-level argument against the doctor's solution would be: 'The doctor acted wrongly because he could get himself into much trouble. They have already punished others for doing the same thing', whereas the argument: 'The doctor acted wrongly because the protection of life is everyone's highest moral obligation. We have no clear moral criteria for distinguishing between mercy-killing and murder' represents a more elaborated argument against the given solution. The moral competence score (C-score) is calculated as the percentage of an individual's total response variation concerning the moral quality of the given arguments (see Lind, 1999; for more information about computing the C-score). The C-score reflects the degree to which a participant's judgments about the pro- and counter-arguments are consistent; the higher the C-score, the greater the moral competence. A highly competent person (indicated by a high C-score close to 100) will consistently appreciate all arguments referring to a certain socio-moral perspective, irrespective of whether this argument is a pro- or counter- argument. In contrast, individuals with low MC will appreciate only arguments that support their own solution of the dilemma (only pro- or counter- arguments, respectively).

2.3. Image acquisition

All imaging was performed on a 3T Trio TIM whole-body MRI scanner (Siemens, Erlangen, Germany). RS-fMRI data were acquired using a gradient-echo echo-planar imaging sequence (TR= 2 s, TE= 24 ms, flip angle= 90°, voxel size= 3.44x3.44x4.00 mm^3, 36 axial slices). Each participant completed one seven-minute RS-fMRI run (i.e., 210 volumes). During the RS-fMRI run, participants were instructed to keep their eyes open. An eye-tracker outsider the scanner was used to monitor participants' eyes, to ensure that they did not fall asleep during the scan. After the functional scans, high-resolution anatomic images were obtained using a T1-weighted 3D MPRAGE sequence (TR= 12.24 ms, TE= 3.56 ms, flip angle= 23°, voxel size= 0.98×0.98×1 mm^3, 192 sagittal slices).

2.4. Image preprocessing

Functional images were preprocessed using SPM8 (www.fil.ion.ucl.ac.uk/spm) and the DPARSFA toolbox (Chao-Gan and Yu-Feng, 2010; www.restfmri.net/forum/DPARSF). After discarding the first five volumes, images were slice-time corrected and realigned. Then, we estimated the amount of noise from physiological and other spurious sources using component-based noise correction (CompCor; Behzadi et al., 2007), which corrects for the noise by regressing out principal components from noise ROIs, such as the white matter (WM) and cerebrospinal fluid (CSF) regions. Global signal regression was not used because it enhances the extent of negative correlations (Murphy et al., 2009). Previous studies suggested that compared to the average signal from WM and CSF regions (i.e., WM/CSF regression methods), principal components derived from these noise ROIs can better account for voxel-specific phase differences in physiological noise (Thomas et al., 2002). The following parameters were included as nuisance regressors within the general linear model: six head-motion parameters and their first derivatives, five principle components from the WM and CSF masks using CompCor, and a linear detrending term. The residual images

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were then normalized in MNI space, and smoothed with a 6-mm full-width at half maximum Gaussian kernel. Finally, a temporal band-pass filter of 0.009–0.08 Hz was applied to the time series. A flowchart of the major steps in data analysis is provided in Figure 1.

2.5. Seed-based functional connectivity analysis

To create seed-based FC maps for the amygdalar network and the FPCN respectively, we defined the left and right amygdala seed ROIs, derived from the Harvard-Oxford subcortical structural atlas (probability threshold 25%), and four spherical seed ROIs of 6 mm radius (rostrolateral prefrontal cortex and anterior inferior parietal lobule for each hemisphere), centered on the coordinates for the FPCN obtained in previous publications (Spreng et al., 2013; see Table 2). For each participant, we extracted the mean time series for each seed and calculated Pearson's correlation coefficients between these mean time series and the time series from all other voxels. These correlation coefficients were converted into Z-values using Fisher r-to-Zvalue transformation. Average Z-maps from 2 seeds of the amygdalar network and from 4 seeds of the FPCN were calculated respectively (i.e., resulting in one mean Z-map per subject for each network). These averaged Z-maps were used for the second-level random-effects analysis in SPM8. We computed one-sample t-tests to determine significant FC maps for each group and each resting-state network. To compare these Z-maps between the two groups, two-sample t-tests with age as a covariate were conducted within the union mask of the one-sample t-test results from each group (i.e., voxels showing significant positive/negative FC maps for either HCSG or LCSG), respectively for positive and negative maps. All statistical results were set at a cluster-level threshold of $p<0.05$, family-wise error (FWE) corrected for multiple comparisons using AlphaSim algorithm implemented in the REST toolbox (http://www.restfmri.net; Song et al., 2011), and a voxel-level threshold of $p<0.001$.

2.6. Inter-network connectivity

To examine the effect of MC on connectivity between the amygdalar network and FPCN, we estimated inter-network connectivity between these two networks by applying the same method described in previous literature (Mamah et al., 2013; Repovs et al., 2011). Based on graph theory, all the ROIs were referred to as "nodes" and the connections among them were considered the "links" within the network. The nodes consisted of 6-mm radius spheres centered on coordinates from previous studies showing the corresponding networks (Luking et al., 2011; Spreng et al., 2013), except for nodes for bilateral amygdala, which were defined by the Harvard-Oxford subcortical atlas; the nodes for each network (9 nodes for the amygdala network and 11 nodes for the FPCN) are presented in Table 2. For each participant, we extracted the mean time series for each of the nodes described above, computed the ROI-to-ROI correlation matrix (20 by 20) using Pearson's correlation, and converted the correlations to Z-values using Fisher r-to-Z transformation. We then computed the average connectivity (mean Fisher Z value) across all ROI-to-ROI connections between two networks as inter-network connectivity. For exploratory purposes, we also computed the average connectivity across node pairs within the same network as intra-network connectivity. Independent-samples t-tests were performed to assess differences in connectivity between the groups. To validate our finding, we further conducted additional inter-network connectivity analyses using nodes derived from an alternative network

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definition for the FPCN and the motor network as a control. The nodes for these networks (21 nodes for the alternative FPCN and 33 nodes for the motor network) were defined as 6-mm radius spheres centered on the coordinates reported in Dosenbach et al. (2010). Then, we estimated the strength of FC between each pair of networks (i.e., the amygdalar network, alternative FPCN, and motor network) and compared FC values between the two groups.

3. Results

3.1. Seed-based functional connectivity results

For seeds in the amygdala and in the FPCN (DLPFC and parietal lobe), we examined whole-brain seed-to-voxel FC patterns (Figure 2). Across both groups, consistent with previous findings (Luking et al., 2011; Kim et al., 2011), the mean time course of the amygdala was positively correlated with the medial frontal regions, including the medial frontal gyrus and the anterior cingulate cortex, insula, thalamus, striatum, superior temporal gyrus, and parahippocampal gyrus (see Table 2). Across both groups, the mean time course in seeds defined for the FPCN was positively correlated with the anterior PFC, DLPFC, dorsomedial PFC, anterior inferior parietal lobule, and anterior insular cortex, which is again consistent with previous research (Vincent et al., 2008; Spreng 2010).

When testing for group differences, we found greater FC between the amygdala seeds and vmPFC for HCSG than for LCSG (peak x, y, z coordinates = −9, 27, −15; t-/z-values = 3.95/3.71; Figure 3). There were no group differences in FC with the FPCN seeds.

3.2. Inter-network connectivity results

In line with our hypothesis, we found less inter-network connectivity between the amygdalar network and FPCN in the HCSG than in the LCSG (mean±SD; 0.048±0.104 vs. 0.108±0.107; t-/p-value = -2.246/0.028; Figure 4). There were no differences between the HCSG and the LCSG in intra-network connectivity (p= 0.5549 for the amygdalar network; p= 0.5827 for the FPCN). In order to validate our finding, we further conducted additional inter-network connectivity analyses with nodes for an alternative FPCN and the motor network as a control (see Materials and Methods). This additional analysis confirmed that there was a significant group difference only in connectivity between the amygdalar network and FPCN, again showing less inter-network connectivity in HCSG than in the LCSG (mean ±SD; 0.025±0.101 vs. 0.074±0.092; t-/p-value = −2.046/0.045; Supplementary Table 1).

4. Discussion

In the present study, we utilized FC analyses of RS-fMRI to examine how individual differences in MC, which assesses the consistent application of moral principles, are associated with intrinsic FC strength in two key networks for emotional and cognitive processing. In accordance with our hypotheses based on prior investigations in the cognitive neuroscience of moral judgment, we found a significant increasein FC between amygdala and vmPFC in HCSG compared to LCSG. In addition, inter-network connectivity between the amygdalar network and FPCN was reduced in HCSG relative to LCSG.

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Neuroimaging and clinical studies have indicated the involvement of the amygdala, vmPFC, and their reciprocal connections in mechanisms underlying moral judgment. For example, many fMRI studies reported increased activity in these regions in response to moral dilemmas such as the trolley problem (Greene et al., 2004), during the making of care-based judgments (Robertson et al., 2007), the passive viewing of pictures displaying moral transgressions (Harenski and Hamann, 2006), and a moral version of the implicit association test (IAT; Luo et al., 2006).

Several studies in psychopaths, individuals with a personality disorder characterized by both antisocial behavior and emotional detachment, showed reduced activity in these regions during moral decision-making (Glenn et al., 2009; Harenski et al., 2014) and the moral IAT (Marsh et al., 2011). In addition, Decety et al. (2012) recently demonstrated increased FC with age (i.e., from childhood to adulthood) between vmPFC and amygdala during the evaluation of moral stimuli. Youths with psychopathic traits, relative to healthy youths, exhibited less amygdala-vmPFC connectivity during the moral IAT (Marsh et al., 2011).

The amygdala is involved in emotional processing and the formation of stimulus-reinforcement associations (LeDoux et al, 1998; Adolphs, 2008) and the vmPFC is involved in reward processing and decision-making (e.g., the representation of value and outcomes; Knutson and Cooper, 2005; Kable and Glimcher, 2009). Particularly, findings from animal studies suggest complementary roles in which the amygdala provides reinforcement expectancy information (both positively and negatively valenced) to the vmPFC/OFC, and this information subsequently is used in the vmPFC/OFC to guide decisions and behavior (Schoenbaum and Roesch, 2005). In line with this notion, Blair (2007) suggested that the amygdala's role in moral judgment is learning the association between actions causing harm to others and the victims' distress (aversive reinforcement) and that the vmPFC plays a crucial role in integrating and modulating amygdala reactivity to stimuli associated with moral transgressions and thus in guiding behavior. Consistent with Blair's (2007) suggestion, one recent study provided evidence for the distinct role of these two regions in moral judgment, showing increased activity in the amygdala and vmPFC when making emotional assessments and integrative judgments of moral dilemmas respectively (Shenhav and Greene, 2014). Shenhav and Greene also demonstrated that the strength of amygdala-vmPFC connectivity varies to the extent to which emotional input is integrated with cognitive processes during moral dilemmas. Taken together, greater amygdala-vmPFC coupling in HCSG may reflect more efficient integration of cognitive and emotional information than in LCSG.

Alternatively, based on previous findings of altered amygdala activity and amygdala-vmPFC/subgenual anterior cingulate cortex (sgACC) connectivity during emotion regulation (Ochsner et al., 2002; 2004; Banks et al. 2007), increased amygdala-vmPFC coupling in HCSG may be related to increased regulation of negative emotion in this group. It has been suggested recently that emotion regulation plays an important role in moral judgment (Hu and Jiang, 2014; Szekely and Miu, 2015a). In a recent behavioral study, the use of strategy to regulate emotion modified moral judgments (Szekely and Miu, 2015b). Specifically, the authors found that cognitive reappraisal reduced the frequency of deontological decisions associated with concerns for rights and duties by decreasing emotional arousal.

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Neuroimaging studies revealed that both the amygdala and vmPFC regions were engaged during moral emotion regulation (Harenski and Hamann, 2006). Hu and Jiang (2014) suggested that the vmPFC recursively appraises (or reappraises) the affective meaning of moral events, generated in the amygdala, while making moral judgments. Taken together, it is possible that regulation of negative emotionselicited by moral dilemmas may reduce the effects of these emotions on moral decisions, enabling more consistent moral judgments.

In the present study, we also found less inter-network connectivity between the amygdalar network (involved in emotional processing) and FPCN (implicated in executive functions and cognitive control) in HCSG relative to LCSG. These two networks appear to operate more independently in HCSG than in LCSG. A recent RS-fMRI study using independent component analysis reported increased inter-network connectivity between the amygdalar network and the FPCN in patients with bipolar disorder (Lois et al., 2014). The study suggested that such increased inter-network connectivity may reflect abnormal integration of affective and cognitive information in the patients and may be related to their impaired emotion regulation. Etkin and colleagues (2009) also revealed increased RSFC between the amygdala and FPCN in patients with generalized anxiety disorder and suggested that such increased RSFC in patients may reflect additional regulatory resources used to compensate for and to diminish their heightened affective responses. Prehn and colleagues (2008) found greater activity in the vmPFC, PSTS, and DLPFC during socio-normative judgments in LCSG relative to HCSG, also suggesting increased recruitment of compensatory resources in this group. Based on these previous findings, we speculate that greater inter-network connectivity in LCSG may reflect less effective cognitive-affective integration, less effective emotional regulation, and corresponding compensatory neural changes, suggesting the importance of the balance between these two networks to produce consistent moral decisions.

In a previous paper in which we reported anatomical data from the same participants (Prehn et al., 2015), we described brain structural differences with regard to Kohlberg's levels of moral development, which is measured with the DIT-2 (Rest et al., 1999). According to Kohlberg's model, individuals at the low levels judge moral issues based on personal interests (pre-conventional level) or social norms (conventional level), whereas individuals at the high level (post-conventional level) judge moral issues based on universal ethical principles (Kohlberg, 1984). In our previous study, we observed greater gray matter volume in the vmPFC/sgACC in individuals with high levels of moral development compared with individuals with low levels of moral development. However, we did not find differences in brain structure between individuals with high and low MC. We suggested that MC might only be represented in functional architecture of the brain but not in structural architecture, as opposed to the moral reasoning schema preferences (i.e., the level of moral reasoning) associated with structural changes. To confirm this suggestion, we also investigated whether there were changes in RSFC according to the level of moral reasoning and did not find any significant changes (not shown).

The present study had some limitations to be addressed in future research. First, according to the aim of the present study, our findings are based on RSFC rather than on brain activity during task performance (i.e., while performing tasks related to information integration or

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emotion regulation). Although spatially distributed activity patterns observed during diverse cognitive tasks are often consistent with resting-state networks, further research needs to be conducted to establish whether the differences in RSFC between HCSG and LCSG also extend to task-evoked activation. Second, it is presently unclear how MC maps on other cognitive abilities such as general intelligence and emotion regulation. Third, although the relative homogeneity of our sample of study participants, designed to remove the effect of education on MC, is a strength of the present study, future research is needed to confirm the present findings in broader samples. Finally, although MC (i.e., C-score) is a continuous variable, our findings were based on differences between individuals at the high and low extremes of MC (i.e., top and bottom 15% of the population), as a first step to find neural differences associated with the level of MC. Thus, our findings raise several questions to be explored by future research. Do the aspects of RSFC where we have identified differences exhibit continuous variation across the full range of MC, or are their discrete differences for individuals of extreme values of MC? Future studies with the entire spectrum are needed to clarify relationships between MC and resting-state networks.

5. Conclusion

We examined whether individual differences in MC are associated with intrinsic FC strength, particularly in the amygdalar network and the FPCN. We found that individuals with higher MC, compared to individuals with lower MC, showed greater amygdala-vmPFC coupling and less inter-network connectivity between the amygdalar network and the FPCN. Our results suggest that RSFC between brain regions associated with emotional-cognitive integration and emotional regulation may contribute to individual differences in competent (i.e., consistent) moral judgment. This study provides first evidence that individual differences in MC are reflected in intrinsic FC networks. Our findings are consistent with current theories emphasizing the role of both emotion and cognition in moral judgment and provide novel insights into how individual differences in moral judgment are linked with FC in brain networks related to emotional and cognitive processing.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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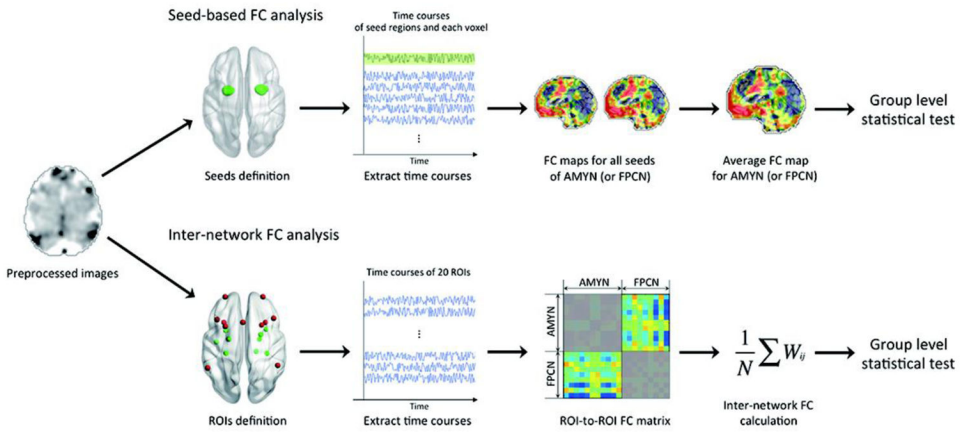

Figure 1.

A flowchart of the major steps in data analysis. Functional connectivity (FC) analyses were conducted using both seed-based FC (top panel) and ROI-based inter-network FC (bottom panel) approaches. After preprocessing resting-state fMRI data, seeds (or regions-of-interests, ROIs) were defined based on a human brain atlas and previous publications (refer to Table 2). The time courses from the above defined seeds and all other voxels in the brain (or those from all ROIs) were extracted and then the correlation coefficients (i.e., FC) between these time courses were calculated. Average FC maps across all maps generated by seeds for each network (or the average connectivity across all FC between AMYN [amygdalar network] and FPCN [fronto-parietal control network] as inter-network FC) were calculated.

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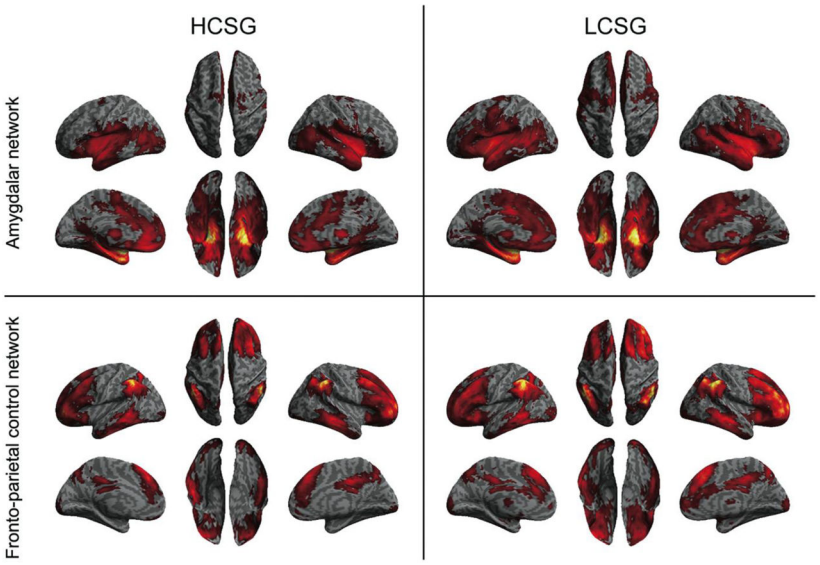

Figure 2.
Significant functional connectivity maps from seeds regions involved in the amygdalar network (top panels) and fronto-parietal control network (bottom panels) in each group.

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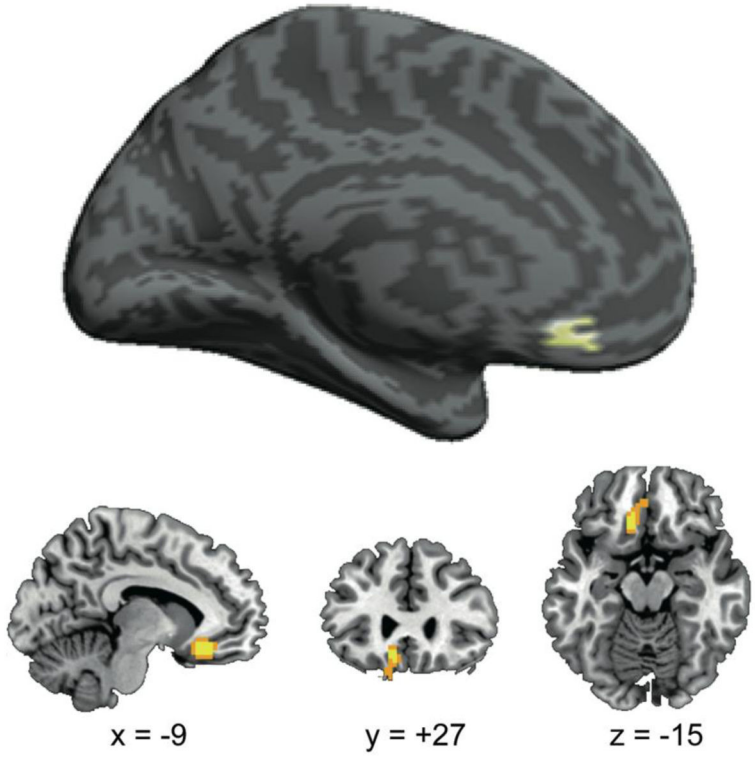

Figure 3.

Regions showing significant differences in the amygdalar network between HCSG and LCSG. HCSG showed greater amygdala-ventromedial prefrontal functional coupling than LCSG.

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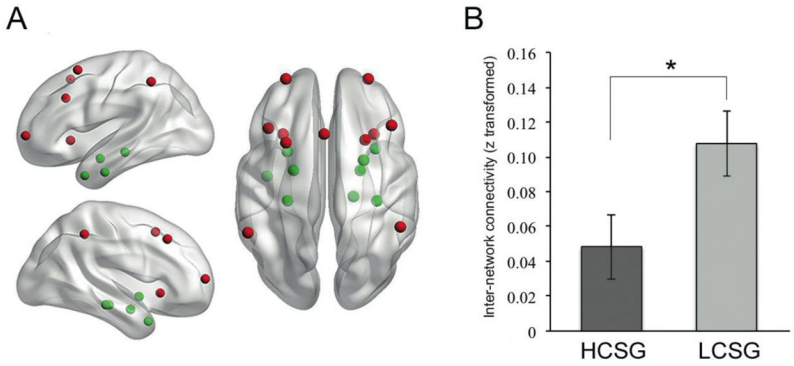

Figure 4.

Result of inter-network connectivity analysis. (A) Figure illustrating the location of regions within each of the amygdalar (green) and fronto-parietal control (red) networks. The coordinates of anatomical regions used for each network are listed in Table 2. (B) Inter-network connectivity differences between HCSG and LCSG. HCSG showed less inter-network connectivity between the two networks than LCSG. *$p<0.05$.

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Table 1

Demographic characteristics and C-score measured using the Moral Competence Test (MCT).

Variable	High C-score group (N = 31)	Low C-score group (N = 33)	p-value
Sex (male/female)	15/16	19/14	0.462
Age (years)	26.68±1.68	27.55±1.56	0.036*
C-score	57.91±8.38 (range 42.74–81.35)	6.61±3.91 (range 0.26–15.33)	p<0.001*

Values are presented as mean ± standard deviation. Asterisks (*) indicate differences between groups (p<0.05).

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Table 2

Regions comprising the fronto-parietal control and amygdalar networks of the brain

Region	MNI coordinates (x, y, z)
Fronto-parietal control network	
Left anterior inferior parietal lobule *	−54, −48, 48
Right anterior inferior parietal lobule *	50, −44, 46
Left anterior insula	−30, 20, −2
Right anterior insula	32, 20, −4
Medial superior prefrontal cortex	−2, 20, 50
Left middle frontal gyrus (BA6)	−28, 14, 58
Right middle frontal gyrus (BA6)	26, 16, 48
Left middle frontal gyrus (BA9)	−40, 24, 34
Right middle frontal gyrus (BA9)	44, 26, 42
Left rostrolateral prefrontal cortex *	−32, 58, 2
Right rostrolateral prefrontal cortex *	32, 58, 8
Amygdalar network [1]	
Left superior temporal gyrus	−27, 6, −32
Right putamen	25, 2, −7
Right parahippocampal gyrus	18, −23, −14
Right superior temporal gyrus	33, 10, −28
Right hippocampus	34, −26, −14
Left inferior temporal gyrus	−41, −9, −29
Left hippocampus	−27, −26, −12

* Seed regions used to define the fronto-parietal control network in seed-based functional connectivity analysis.

[1] Bilateral amygdalae defined from the Harvard-Oxford subcortical atlas were also included as nodes for the amygdalar network.