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Volitional regulation of emotions produces distributed alterations in connectivity between visual, attention control, and default networks

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ABSTRACT

The ability to volitionally regulate emotions is critical to health and well-being. While patterns of neural activation during emotion regulation have been well characterized, patterns of connectivity between regions remain less explored. It is increasingly recognized that the human brain is organized into large-scale intrinsic connectivity networks (ICNs) whose interrelationships are altered in characteristic ways during psychological tasks. In this fMRI study of 54 healthy individuals, we investigated alterations in connectivity within and between ICNs produced by the emotion regulation strategy of reappraisal. In order to gain a comprehensive picture of connectivity changes, we utilized connectomic psychophysiological interactions (PPI), a whole-brain generalization of standard single-seed PPI methods. In particular, we quantified PPI connectivity pair-wise across 837 ROIs placed throughout the cortex. We found that compared to maintaining one's emotional responses, engaging in reappraisal produced robust and distributed alterations in functional connections involving visual, dorsal attention, frontoparietal, and default networks. Visual network in particular increased connectivity with multiple ICNs including dorsal attention and default networks. We interpret these findings in terms of the role of these networks in mediating critical constituent processes in emotion regulation, including visual processing, stimulus salience, attention control, and interpretation and contextualization of stimuli. Our results add a new network perspective to our understanding of the neural underpinnings of emotion regulation, and highlight that connectomic methods can play a valuable role in comprehensively investigating modulation of connectivity across task conditions.

Introduction

The ability to volitionally regulate emotion contributes to behavioral flexibility and well-being, while deficits in this capacity are linked to maladjustment and psychopathology (Gross and Thompson, 2007). Given its importance in health and disease, more than 50 studies have examined the neural mechanisms of emotion regulation with functional magnetic resonance imaging (fMRI). These studies demonstrate that emotion regulation involves increased activity in cortical regions associated with cognitive and attention control such as dorsomedial prefrontal cortex (PFC), lateral PFC, and superior parietal regions, and produces diminished activation in emotion production regions such as the amygdala (see Ochsner and Gross, 2005; Ochsner et al., 2012; Phan and Sripada, 2013 for reviews). Though patterns of activation during emotion regulation have been well characterized, patterns of connectivity between regions remain less explored.

The issue of connectivity alterations during emotion regulation is particularly intriguing in light of increasingly influential network models of neural architecture. The human brain appears to be organized into large-scale intrinsic connectivity networks (ICNs) (Fox et al., 2005; Menon, 2011). These are distributed regions that exhibit coherent activity during rest and tasks (Greicius et al., 2003; Smith et al., 2009) and are associated with specific neurocognitive functions (Laird et al., 2011). Alterations in the relationships between ICNs during tasks are thought to reflect adjustments in network-mediated information-processing

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(Bressler and Menon, 2010), and are predictive of task performance (Fransson, 2006). While the ICN perspective has primarily been applied to studies of the unperturbed resting state, a growing body of research investigates network alterations produced by psychological tasks (Fornito et al., 2012; Harrison et al., 2008; Kinnison et al., 2012; Spreng et al., 2010).

In social affective neuroscience, challenges have emerged for "faculty approaches" that seek to localize particular emotions and emotion regulatory capacities in discrete brain regions (Barrett and Satpute, 2013; Lindquist et al., 2012). A new "network-based approach" (Barrett and Satpute, 2013; Kinnison et al., 2012) instead investigates affective phenomena from a distributed systems perspective. In this framework, emotions are conceptualized as mental events that emerge from integration within and between large-scale networks. Recent studies have uncovered altered network interrelationships due to social affective phenomena such as emotion states (Barrett and Satpute, 2013; Eryilmaz et al., 2011), moods (Harrison et al., 2008), and empathy (Raz et al., 2013). Applying a network-based perspective to understanding emotion regulation, it is plausible that this capacity implicates a number of constituent processes associated with large scale ICNs. These include visual processing (visual network; Yeo et al., 2011), voluntary control of visual attention (dorsal attention network; Corbetta and Shulman, 2002), working memory and goal-directed attention (frontoparietal network; Seeley et al., 2007), and assigning personal meanings to stimuli (default network; Buckner et al., 2008; Gusnard et al., 2001). These observations raise the hypothesis that these implicated ICNs alter their relationships, and in particular, become more interconnected, during voluntary regulation of emotion, reflecting greater integration of information across these constituent processes.

In this fMRI study of 54 healthy individuals, we investigated alterations in connectivity within and between large-scale networks produced by reappraisal, an important voluntary emotion regulation strategy. Previous studies of connectivity during emotion regulation have used seed-based methods, and examined a single or small number of seeds (Banks et al., 2007; Urry et al., 2006; Wager et al., 2008). These methods have clarified links between subcortical nodes, especially amygdala and striatum, and prefrontal regions implicated in regulation. They are less useful, however, for identifying altered relationships across large-scale ICNs. Thus in order to gain a comprehensive picture of large-scale network changes produced by emotion regulation, we utilized connectomic psychophysiological interactions (PPI), a whole-brain generalization of standard single-seed PPI methods (Friston et al., 1997; McLaren et al., 2012). We quantify PPI connectivity pairwise across 837 ROIs placed throughout the cortex. We utilize network contingency analysis, a statistical method that identifies connectivity changes across pairs of networks. We demonstrate that voluntary regulation of emotion produces robust and distributed alterations in interconnections between multiple networks implicated in current theoretical models of emotion regulation.

Methods

Subjects

All subjects provided informed consent for the study protocol, as approved by the University of Michigan Institutional Review Board. Of 54 participants who entered the study, two did not complete the task, one had incomplete fMRI data due to scanner problems, and two had excessive head movement during scanning (>3 mm movement). Thus 49 participants contributed to the present analysis (age mean and sd: 23.63 ± 1.30, range: 20–27, males = 26). All subjects had no MRI contraindications (e.g., metallic/ferrous materials in their body), no prior or current treatment for any psychiatric disorder (clinician-conducted psychiatric evaluation based on the Structured Clinical Interview for DSM-IV), and no history of neurological injury.

Participants for this study were recruited as part of an fMRI study of the long-term neural effects of childhood poverty. At the time of scanning, 15% of subjects were below the U.S. Census Bureau-defined poverty line, which is similar to a representative sample of U.S. residents. At age 9, roughly half of the participants were from households below the U.S. Census Bureau-defined poverty line, and the other half were from non-poverty backgrounds. See Evans (2003) for further details on subject recruitment and protocols. In the present study, our primary interest was in the effects of emotion regulation on network connectivity, rather than effects of childhood poverty. We included covariates controlling for the effects of current income and childhood poverty in all analyses.

Task

We used an Emotion Regulation Task (ERT) validated in previous fMRI studies (Banks et al., 2007; Phan et al., 2005). The task involved three conditions. During the Maintain and Reappraise conditions, participants were presented with aversive pictures from the International Affective Picture System (IAPS; Bradley and Lang, 2007). During the Maintain condition, participants were instructed to attend to and experience naturally (without trying to change or alter) the emotional state elicited by the pictures. During the Reappraisal condition, participants were instructed to voluntarily decrease the intensity of their negative affect by using the cognitive strategy of reappraisal (Gross, 1999). In particular, participants were asked to use one of two strategies: 1) transforming the depicted scenario into less negative or positive terms (e.g., people crying outside the church are leaving a wedding and the tears are joyful); and 2) rationalizing or objectifying the content of the pictures (e.g. an abused woman is an actress in a movie between scenes). During a pre-scanning session, participants practiced these reappraisal strategies by talking through the process out loud with practice stimuli (separate from the stimuli shown in the scanning session). Experimenters assisted participants by correcting their technique or suggesting alternative reappraisals. Participants were instructed not to look away or distract themselves with irrelevant thoughts. Participants practiced until they could reliably and rapidly generate appropriate reappraisals of stimuli, and understanding of the task was confirmed by reviewing examples of subject-generated strategies. There was also a third condition, the Neutral Look condition, in which participants were presented with neutral IAPS pictures and instructed to simply look at them. This condition provided a control condition for an additional hypothesis, unrelated to the aims of the current report, of the effects of childhood poverty on neural responses to aversive pictures. Of note, we chose to study reappraisal because it is an important emotion regulation strategy (Gross, 1999), has been shown to produce beneficial psychological and physiological changes (Gross, 1998), and has been validated in fMRI in multiple prior studies (Ochsner et al., 2002; Phan et al., 2005; see Ochsner et al., 2012; Phan and Sripada, 2013 for reviews).

The fMRI task was structured in terms of a block-related design in which subjects viewed 20 second blocks of aversive or neutral pictures. Each picture was presented continuously for 5 s without an interstimulus interval. Prior to each block of pictures, the instruction to 'Look', 'Maintain' or 'Reappraise' appeared at the center of a black screen for a duration of 5 s (Instruction). Immediately following each Neutral Look, Maintain or Reappraise block, a blank screen with a rating scale appeared for 5 s asking participants to rate the intensity of their negative affect on a 5-point scale (1 = least negative/neutral, 5 = extremely negative) via button response (Rating). The Look/Maintain/Reappraise blocks were interspersed with 20 second baseline blocks consisting of a fixation cross to minimize carryover effects ('Baseline'), and to allow the blood oxygen-level dependent (BOLD) signal to return to baseline. During this period, participants were asked to stop maintaining or reappraising their emotional experience and to relax. The total task duration was 10 min spread across 2 runs.

The stimulus set consisted of 32 highly aversive and arousing pictures and 16 neutral pictures based on normative IAPS ratings (Bradley and