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Intrinsic connectivity in the human brain does not reveal networks for 'basic' emotions

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We tested two competing models for the brain basis of emotion, the basic emotion theory and the conceptual act theory of emotion, using resting-state functional connectivity magnetic resonance imaging (rs-fcMRI). The basic emotion view hypothesizes that anger, sadness, fear, disgust and happiness each arise from a brain network that is innate, anatomically constrained and homologous in other animals. The conceptual act theory of emotion hypothesizes that an instance of emotion is a brain state constructed from the interaction of domain-general, core systems within the brain such as the salience, default mode and frontoparietal control networks. Using peak coordinates derived from a meta-analysis of task-evoked emotion fMRI studies, we generated a set of whole-brain rs-fcMRI 'discovery' maps for each emotion category and examined the spatial overlap in their conjunctions. Instead of discovering a specific network for each emotion category, variance in the discovery maps was accounted for by the known domain-general network. Furthermore, the salience network is observed as part of every emotion category. These results indicate that specific networks for each emotion do not exist within the intrinsic architecture of the human brain and instead support the conceptual act theory of emotion.

Keywords: emotions; intrinsic functional connectivity networks; basic emotion theory; conceptual act theory of emotion

INTRODUCTION

For the past 50 years, scientists have been largely convinced that certain emotions, such as anger, fear, sadness, happiness and disgust, are biologically basic, meaning that they are natural kinds (Barrett, 2006). In this view, each emotion category arises from an innate, specific brain module with homology to other animals [e.g. (Ekman, 1999; Keltner and Ekman, 2000; Tracy and Randles, 2011)][1]. This basic emotion view has dominated the science of emotion, and is widely accepted in the popular media, despite the fact the brain basis of emotion is still poorly understood. Although careful and elegant studies of so-called 'emotional' behavioral adaptations in non-human animals have revealed distinct neural circuits that control escape (Vazdarjanova and McGaugh, 1998), freezing (LeDoux, 2007) and fighting [e.g. offensive attack (Lin *et al.*, 2011); defensive aggression (Motta *et al.*, 2009)], there are a number of arguments for why a neural circuit for a behavior cannot be considered a neural circuit for an emotion *per se* [e.g. (Barrett *et al.*, 2007; Barrett, 2012; LeDoux, 2012)]. For example, depending on the circumstances, an animal might flee, freeze or fight when faced with potential danger (i.e. during a 'fearful' situation). This introduces the problem of having many fear circuits [e.g. (Gross and Canteras, 2012)] and poses an inductive problem for the science of basic emotions. Cognitive neuroscience and lesion research has searched for emotion brain modules with little success [for recent meta-analytic evidence, see (Kober *et al.*, 2008; Lindquist *et al.*, 2012); for a discussion, see (Lindquist and Barrett, 2012; Barrett and Satpute, 2013)]. One recent meta-analysis of the human neuroimaging literature was interpreted as supportive of the basic emotion hypothesis (Vytal and Hamann, 2010), but in fact reported limbic and non-limbic regions as showing consistent but non-specific increases in activation during anger, sadness, fear, disgust and happiness [for an alternative interpretation of their findings see (Hamann 2012; Lindquist *et al.*, 2012)].

In contrast to the basic emotion view, a constructionist approach to emotion, the 'conceptual act theory of emotion' hypothesizes that an emotion such as anger, sadness, fear, disgust or happiness is a population of instances; the instances do not arise from their own, dedicated brain network, but are instead constructed from the combination of activity in domain-general, core brain systems that perform more basic psychological functions such as salience detection, memory, sensory perception, language and so on (Barrett, 2006, 2012; Lindquist and Barrett, 2012; Barrett and Satpute, 2013). In particular, the conceptual act theory of emotion predicts that the same intrinsic networks would be engaged during a variety of emotions, although perhaps in different patterns [for an extension of this view see (Oosterwijk *et al.*, 2012)]. Indeed, preliminary support for the conceptual act theory of emotion view can be observed in several recent neuroimaging experiments (Wilson-Mendenhall *et al.*, 2011, 2013) demonstrating the involvement of brain areas associated with representing body states, salient events, memory, sensory perception and language during emotional experiences. Other evidence consistent with the conceptual act theory of emotion comes from intracranial stimulation studies (Guillory and Bujarski, 2014) as well as meta-analyses of neuroimaging experiments demonstrating that domain-general brain systems are

[1] For example, Ekman (1999) wrote 'It is necessary to posit emotion-specific central nervous system (CNS) activity in my account of basic emotions. The distinctive features of each emotion, including the changes not just in expression but in memories, imagery, expectations and other cognitive activities, could not occur without central nervous system organization and direction. There must be unique physiological [CNS] patterns for each emotion' (p. 50). More recently, in a review of basic emotion theories, Tracy and Randles (2011) wrote that an 'agreed-upon gold standard is the presence of neurons dedicated to the emotion's activation' (p. 398).

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commonly engaged across a variety of emotion categories (Lindquist *et al.*, 2012) and during both emotional and cognitive events (Lindquist and Barrett, 2012; Barrett and Satpute, 2013).

In this study, we compared the 'basic emotion' and 'conceptual act' theories using an analysis of the brain's intrinsic functional connectivity. A recent explosion of research demonstrates that the human brain contains a small world architecture with densely connected 'hubs' (Sporns, 2013; van den Heuvel and Sporns, 2013). Within this structure, the brain shows continuous, intrinsic activity organized as connected networks. These networks, referred to as 'intrinsic networks', are identified in temporal correlations of the low-frequency blood oxygen level-dependent (BOLD) signal fluctuations in voxels while a participant lays 'at rest' during functional magnetic resonance imaging (called 'resting-state functional connectivity magnetic resonance imaging' or rs-fcMRI). Critically, patterns of intrinsic activity are quite similar to the patterns of task-related activity [(Smith *et al.*, 2009; Spector *et al.*, 2009); for a review see (Bressler and Menon, 2010)]. These networks also account for a large proportion of the brain's metabolic budget (Raichle, 2010). Together, these findings have thus led researchers to conclude that spontaneous neuronal activity within these networks reflects the intrinsic organization of the brain (Buckner *et al.*, 2013), which in turn forms the functional architecture of the mind (Menon, 2011; Lindquist and Barrett, 2012; Barrett and Satpute, 2013;).

There are several reasons why intrinsic brain networks are useful for comparing the basic emotion and conceptual act theories. First, intrinsic brain networks have anatomic and cross-species properties that make rs-fcMRI an ideal approach for testing the basic emotion theory's hypothesis that dedicated emotion networks exist. Intrinsic networks are anatomically constrained (van den Heuvel *et al.*, 2009; Deco *et al.*, 2010; Pernice *et al.*, 2011; Hermundstad *et al.*, 2013), and can be observed under anesthesia (Greicius *et al.*, 2008). The networks are found in people of different cultures [e.g. (Manoliu *et al.*, 2013; Wang *et al.*, 2014)]. Several of the networks are homologous with the networks that exist within the brains of other animals (Rilling *et al.*, 2007; Vincent *et al.*, 2007; Hayes and Northoff, 2011; Mantini *et al.*, 2013). By comparison, basic emotion theory hypothesizes that (i) each emotion is caused by a specific, dedicated network that is anatomically intrinsic to the human brain, (ii) each network should be universal and (iii) homologous in non-human animals. Furthermore, some theories propose that these networks should be confined to subcortical regions of the brain [e.g. (Panksepp, 1998)], making it difficult to identify them in studies of humans where direct anatomical investigations are difficult. Second, many rs-fcMRI studies reveal the existence of domain-general intrinsic networks; these can be used to test the conceptual act theory's hypothesis that an emotion is constructed as an interaction of domain-general systems. To date, networks have been identified for salience (Seeley *et al.*, 2007; Touroutoglou *et al.*, 2012), language (Lohmann *et al.*, 2010; Tomasi and Volkow, 2012), executive function (Seeley *et al.*, 2007; Vincent *et al.*, 2008), attention (Corbetta *et al.*, 2008; Vincent *et al.*, 2008), semantic processing (Binder *et al.*, 2009), memory (Buckner *et al.*, 2008; Dickerson and Eichenbaum, 2010) and other processes [(Yeo *et al.*, 2011) for a review see (Bressler and Menon, 2010)]. If emotions are constructed as interactions of basic networks that subserve domain-general functions in the brain, then rs-fcMRI analyses should reveal (i) evidence of many intrinsic networks contributing to a single instance of an emotion category and (ii) evidence of a common intrinsic network contributing to different emotion categories. Thus, the rs-fcMRI approach, while not a perfect window into the structure within the human brain, does allow an opportunity to investigate the structural properties of the brain in relation to emotion.

Although a number of intrinsic networks have now been replicated across samples and analysis methods [e.g. seed-based rs-fcMRI (Vincent *et al.*, 2008); independent components analysis (Smith *et al.*, 2009)], no studies to date have explicitly used rs-fcMRI to examine whether a specific intrinsic connectivity network can be identified for each emotion category.

In this study, we thus used a 'seed and discover' method (Vincent *et al.*, 2008) to assess whether there are specific intrinsic networks for specific emotions or whether the networks underlying emotional experiences and perceptions are comprised as combinations of domain-general intrinsic networks such as those found in Shirer *et al.* (2012), Yeo *et al.* (2011) and Smith *et al.* (2009) (e.g. networks involved in salience detection, memory, attention, language, motor function and sensation). The 'seed and discover method' relied on two types of evidence: meta-analytic data and resting-state data. (i) Meta-analytic peaks of task-evoked fMRI activity; these identified a priori regions of interest (ROIs) that consistently showed an increase in activity during emotional experiences and emotion perception. (ii) These peaks were then used as 'seeds' in the analysis of rs-fcMRI data from two samples to generate the intrinsic 'discovery' maps for each emotion category (Sample 1, $N = 89$; Sample 2, $N = 300$). In particular, we extracted the time course of BOLD activity from a predefined 'seed' region and compared it to the time course of all other voxels in the brain. The result was a 'discovery' map of voxels that showed a similar BOLD response across time. Voxels whose time courses correlate significantly with one another are considered to be part of the same rs-fcMRI intrinsic network.

To investigate whether intrinsic networks exist for anger, disgust, fear, sadness and happiness, we chose ROI seeds from the activation peaks reported in Vytal and Hamann's (2010) meta-analysis of task-related functional neuroimaging studies of emotion experience and perception (see Table 1). In contrast to resting-state functional connectivity analyses, task-evoked fMRI studies reveal brain regions that show increases in activation (relative to some baseline condition) during specific psychological tasks or conditions (e.g. experiencing anger relative to a neutral emotional state). Meta-analyses of task-evoked activity overcome the Type I error prevalent in individual task-evoked fMRI studies by revealing those brain areas that consistently show increases in activity during a particular condition (e.g. anger) across studies (cf. Lindquist *et al.* 2012). Using the activation likelihood estimation meta-analytic method, Vytal and Hamannn (2010) thus identified regions that were consistently activated across studies for each of the five emotion categories (anger, sadness, fear, disgust and happiness).

If anatomically constrained networks for each emotion category exist in the intrinsic architecture of the human brain, as the basic emotion view predicts, then the meta-analytically derived seed regions for a given emotion category (i.e. the peaks of consistent activation for a given category of emotion, such as happiness) should produce 'discovery' maps whose spatial overlap reveals a network for that category. This finding would provide strong support for the hypothesis that emotions are biologically basic categories reflected in the intrinsic structure of the brain. Alternatively, if the peaks observed in Vytal and Hamannn (2010) are nodes in domain-general intrinsic networks, as predicted by the conceptual act theory of emotion, then the conjunction of the discovery maps for a given emotion category would not converge on a single network. Instead, emotion-based seeds would give evidence of the domain-general intrinsic networks that are already known to exist in the literature.

To ascertain the degree of spatial overlap between the discovery maps that were generated by the meta-analytically derived emotion seeds and the maps for well-known domain-general intrinsic networks (i.e. visual, language, episodic memory, executive function, salience detection networks) (Yeo *et al.*, 2011; Shirer *et al.*, 2012), we used a goodness-of-fit metric (Greicius *et al.*, 2004). The conceptual act

Table 1 Seed regions of interest

Label	MNI Coordinates		
	x	*y*	*z*
Happiness			
Right superior temporal gyrus (R STG)*	48	−55	−4
Left anterior cingulate cortex (L ACC)	−2	43	7
Left cerebellum	−40	−63	−25
Anger			
Left inferior frontal gyrus (L IFG)*	−45	23	−3
Right parahippocampal gyrus (R PHG)	19	−20	−11
Left fusiform gyrus	−44	−72	−18
Fear			
Left amygdala *	−23	−6	−11
Right amygdala	23	−10	−14
Right cerebellum	33	−54	−15
Right insula	43	3	−2
Sadness			
Left medial frontal gyrus (L medFG)*	−4	47	32
AmygdaRight inferior frontal gyrus (R IFG)	40	6	23
Left caudate head	−10	19	−9
Disgust			
Right inferior frontal gyrus/insula (rIFG/insula)*	31	5	−4
Left inferior frontal gyrus/insula (rIFG/insula)	−26	29	−10
Left lingual gyrus	−22	−72	−11
Left amygdala	−20	−3	−17

Note: This article used a set of three different regions found to be consistently active during each emotion category previously reported in the Vytal and Hamann (2010) meta-analysis of task-induced emotion activations. We selected the three peak activations with the largest cluster of activation for happiness, anger, and sadness. We included four peaks of activation for fear and disgust because the two peaks with the largest cluster of activation were both within the same brain region in different hemispheres. The set of regions for emotions are listed in rank order, based on the size of meta-analytic cluster of activation (*indicates the regions with the largest activation peak for each emotion). All coordinates are referenced to the MNI coordinate system.

theory of emotion hypothesizes that emotional instances are constructed from the interactions of these domain-general networks. According to this hypothesis, the brain predicts incoming sensory input from the body and the world by categorizing it, thereby constructing it into meaningful emotional experiences and perceptions (Barrett, 2009, 2012; Lindquist and Barrett, 2012; Barrett, 2013, 2014). From this perspective, the salience, default mode network (DMN) and frontoparietal control networks are centrally important to constructing instances emotion (being involved in interoception, semantic processing and categorization, respectively), but so too are the exteroceptive and other attention networks as well. An instance of emotion is understood as a brain state, constructed as the ongoing interaction of brain networks.

Finally, we also assessed the conceptual act theory of emotion hypothesis that all emotions constructed with the 'salience network'. The strength of connectivity within this network is correlated to the intensity of affective experience (Seeley *et al.*, 2007; Touroutoglou *et al.*, 2012, 2014) and nodes within this network show an increase in activation across varying instances of emotions in task-evoked studies (Wilson-Mendenhall *et al.*, 2013). Furthermore, this network is particularly relevant to negative emotions (Seeley *et al.*, 2007; Hayes and Northoff, 2011; Bickart *et al.*, 2012; Touroutoglou *et al.*, 2012, 2014). To test this hypothesis, we used the same seed and discover method to determine whether there was any spatial overlap between the 'discovery' maps for anger, sadness, fear and disgust. Support for basic emotion theory would be found if the different negative emotion categories each had a distinct network. Support for the conceptual act theory of emotion would be found if the different negative emotion categories had overlapping regions within a common network such as the salience network.

MATERIALS AND METHODS

Participants

Sample 1 consisted of 89 young adults (44 men) ranging in age from 18 to 33, with a mean age of 22.4 years (s.d. = 3.34). Sample 2 consisted of 300 young adults (150 men) with a mean age of 22.3 years (s.d. = 1.94) (rs-fcMRI data from both samples have been previously published in Yeo *et al.*, 2011). All participants were right-handed, native English speakers and had normal or corrected-to-normal vision. No participant reported a history of neurological or psychiatric disorder.

fMRI data acquisition and preprocessing procedures

Data were collected with a 3 T Tim Trio System (Siemens Medical Systems, Erlangen, Germany), using a 12-channel phased-array head coil. Structural data in Sample 1 and 2 were acquired using a 3D T1-weighted magnetization-prepared gradient-echo image [repetition time (TR) = 2200 ms; echo time (TE) = 1.54 ms; flip angle (FA) = 70°, 1.2 mm isotropic voxels]. Whole-brain fMRI data were acquired with echo-planar sequence [Sample 1 and Sample 2: TR = 3000 ms; TE = 30 ms; FA = 90°; 3.0 mm isotropic voxels, 47 slices]. During the resting-state fMRI runs, participants were instructed to keep their eyes open. Head motion was minimized using head restraints, including a pillow and foam padding. Noise was attenuated with ear plugs.

Preprocessing of the fMRI data involved a series of previously established rs-fcMRI procedures (Van Dijk *et al.*, 2010), including (i) removal of the first four volumes to allow for T1 equilibration effects, (ii) slice timing correction (SPM2, Wellcome Department of Cognitive Neurology, London, UK) and (iii) head motion correction [Functional MRI of the Brain (FMRIB), Oxford, UK]. Data were normalized to the Montreal Neurological Institute (MNI) atlas space (SPM2, Wellcome Department of Cognitive Neurology, London, UK) and resampled to 2-mm cubic voxels. A low-pass temporal filter removed frequencies higher than 0.08 Hz. Data were spatially smoothed using a 6-mm full-width half-maximum Gaussian filter. Sources of spurious variance and their temporal derivatives were removed through linear regression including (i) six parameters obtained by rigid-body correction of head motion correction, (ii) the signal averaged over the whole brain, (iii) the signal averaged over the ventricles and (iv) the signal averaged over the deep cerebral white matter.

Functional connectivity analysis

Selection of ROIs

The atlas coordinates of all seed ROIs are presented in Table 1. To examine whether emotion seed ROIs reveal intrinsic emotion networks, we used peak activations that were more consistent than expected by chance for each emotion within the Vytal and Hamann (2010) meta-analysis (for the validity of this 'seed and discover' method see Supplementary Materials). As the seeds for the discovery maps, we selected the peak activations of three different regions with the largest cluster of activation for each emotion category. Our rationale was that these ROIs would constitute the most spatially discriminable regions for each presumed 'basic' emotion. For ease of reporting, we only present the analysis using the three largest peak activations (i.e. those showing the highest degree of consistency among individual studies in the literature) reported for each emotion in Vytal and Hamannn (2010). To ensure that the number of peaks analyzed did not affect the analysis, we also performed a 'seed and discover' analysis using all peak activations reported for each emotion in Vytal and Hamannn (2010) (9–19 peaks per emotion) (see Supplementary Figures S2–S4).

Overlapping spatial topography of the rs-fcMRI discovery maps

To create each 'discovery' map, we created spherical ROIs (4 mm radius) around each seed region and then computed Pearson's product moment correlations (r) between the mean signal time course of each seed region and the time course of all other voxels in the brain. The resulting correlation maps were converted to z-values, using Fisher's r-to-z transformation and were averaged across participants. To explore whether each set of seed regions revealed a unified intrinsic connectivity network, we next computed a spatial conjunction analysis on the discovery maps for each emotion category. Specifically, the group-level z-score maps for the seed reference regions were binarized at a minimum threshold of $z(r) = 0.25$. We then computed their convergent spatial overlap, identifying voxels with $z(r)$ values ≥ 0.25 in all seed regions. All maps are shown on slices in MNI atlas space using the FSL view toolbox (http://www.fmrib.ox.ac.uk/fsl) (for the validity of this method see Supplementary Materials).

In addition to generating spatial convergence maps, we quantified the strength of functional connectivity between the seed regions by calculating Fisher's r-to-z correlation coefficients between each pair of seeds. Next, we calculated the average connectivity measure of $z(r)$ values between the seeds associated with the three seeds for each emotion category. As a reference range for functional connectivity strength values, we calculated the average connectivity measure of $z(r)$ values within the well-known 'DMN' [e.g. (Andrews-Hanna *et al.*, 2010) (see Supplementary Materials)]. As a control analysis, we selected seed ROIs in visual, motor and auditory cortex that are typically uncorrelated (as in Van Dijk *et al.*, 2010) (see Supplementary Materials).

To test the hypothesis that seed regions from each negative emotion were part of the same intrinsic rs-fcMRI network [i.e. the salience network (Seeley *et al.*, 2007)], we examined the conjunction of the discovery maps for the single largest (i.e. most spatially distinctive) meta-analytic peak for each discrete negative emotion (see Table 1).

Goodness-of-fit analysis between the rs-fcMRI emotion maps and primary intrinsic connectivity networks

To test the hypothesis that the emotion seed regions produced rs-fcMRI maps that were representative of canonical intrinsic connectivity networks, we calculated a goodness-of-fit metric (Greicius *et al.*, 2004) that represented a spatial similarity index over the entire map. For this analysis, we chose a set of 14 intrinsic connectivity networks identified by Shirer *et al.* (2012) (Table 2; see also Figure 2S in Shirer *et al* (2012). Because the 'salience network' plays a critical role in affective experience (Seeley *et al.*, 2007; Touroutoglou *et al.*, 2012, 2014), we included the dorsal salience subnetwork [most clearly involving connections between the dorsal anterior insula and dorsal anterior cingulate cortex (ACC)] and the ventral salience subnetwork network (involving connections between ventral anterior insula and pregenual ACC extending to the subgenual ACC) identified by Touroutoglou *et al.* (2012). The canonical intrinsic connectivity networks of interest included in this analysis are presented in Table 2.

Table 2 Intrinsic connectivity networks of interest used for the goodness-of-fit analysis

Dorsal and ventral salience networks identified by Touroutoglou *et al.* (2012)
1. Dorsal anterior insula network (Dorsal Salience)
2. Ventral anterior insula network (Ventral Salience)

Intrinsic connectivity networks identified by Shirer *et al.* (2012)
1. Insula/dorsal ACC (Anterior Salience)
2. Posterior insula (Posterior Salience)
3. Auditory
4. Basal ganglia
5. PCC/Medial prefrontal cortex (dorsal DMN)
6. Retrosplenial cortex/medial temporal lobe (ventral DMN)
7. Language
8. Left dorsolateral prefrontal cortex/Left parietal lobe (Left executive control network, ECN)
9. Right dorsolateral prefrontal cortex /Right Parietal Lobe (Right executive control network, ECN)
10. Intraparietal sulcus/Frontal Eye Field (Visuospatial)
11. Precuneus
12. Primary visual cortex,V1
13. Secondary visual cortex,V2 (High-level visual)
14. Sensorimotor

A template of each of the intrinsic connectivity networks of interest was used to select the 'best-fit' of rs-fcMRI emotion maps. We used the template-matching procedure developed by Greicius *et al.* (2004) that involved taking the average z score of voxels falling within the template minus the average z score of voxels outside the template and selecting the network of interest in which this difference (the goodness-of-fit) was the greatest. As a reference range for goodness-of-fit values, we calculated the goodness-of-fit metric between the rs-fcMRI DMN maps and the canonical intrinsic connectivity networks (see Supplementary Materials). We expected the rs-fcMRI DMN discovery maps to have high fit values with dorsal and ventral DMN but low fit values with the sensorimotor, auditory or visuospatial networks identified by Shirer *et al.* (2012).

Reliability of rs-fcMRI emotion maps

To assess the reliability of the strength of connectivity of the rs-fcMRI emotion maps, we computed intraclass correlation coefficients (ICC) (two-way random effects with absolute agreement) between the connectivity $z(r)$ values between the trio of seeds associated with each emotion category in Samples 1 2, using PASW Statistics 18, Release Version 18.0.0 (SPSS, Inc., 2009, Chicago, IL, www.spss.com).

RESULTS

Peaks of consistent activity during emotion belong to domain-general intrinsic networks

Inconsistent with the basic emotion hypothesis and consistent with the conceptual act theory of emotion hypothesis, we did not find strong evidence for intrinsic networks corresponding to specific emotions (Figure 1). For instance, the anger peak discovery maps (created from three of the largest meta-analytic activation peaks from Vytal and Hamann, 2010 and the voxels correlated with each peak) did not share spatial overlap with one another. As a result, the conjunction of the anger discovery maps was empty, indicating that an anatomically constrained network for anger does not exist within the intrinsic architecture of the human brain. Neither 'discovery' maps at our a priori threshold of $z(r) = 0.25$, nor maps at a less stringent threshold of $z(r) = 0.1$, revealed an intrinsic network. We repeated this analysis, with the same result, for the peaks that consistently activated in Vytal and Hamann's analysis during sadness, fear, disgust and happiness. The average connectivity strength, $z(r)$, between the seed regions for the five emotions are shown in Figure 2. Furthermore, when we repeated the analysis using a larger number of seeds from all the meta-analytic peaks available in Vytal and Hamannn (2010), the results did not change. Specifically, 13 peaks that were consistently activated during anger, 19 peaks that were consistently activated during sadness, 10 peaks that were consistently activated during fear, 16 peaks that were consistently activated for disgust and 9 peaks that were consistently activated during happiness in Vytal and Hamannn (2010) meta-analysis did not together reveal an intrinsic network for each emotion category (see Supplementary Figures S2 and S3).

Instead, the goodness-of-fit analysis revealed that Vytal and Hamann (2010)'s peaks were nodes in the set of domain-general intrinsic networks already identified in the literature (Table 3; see also

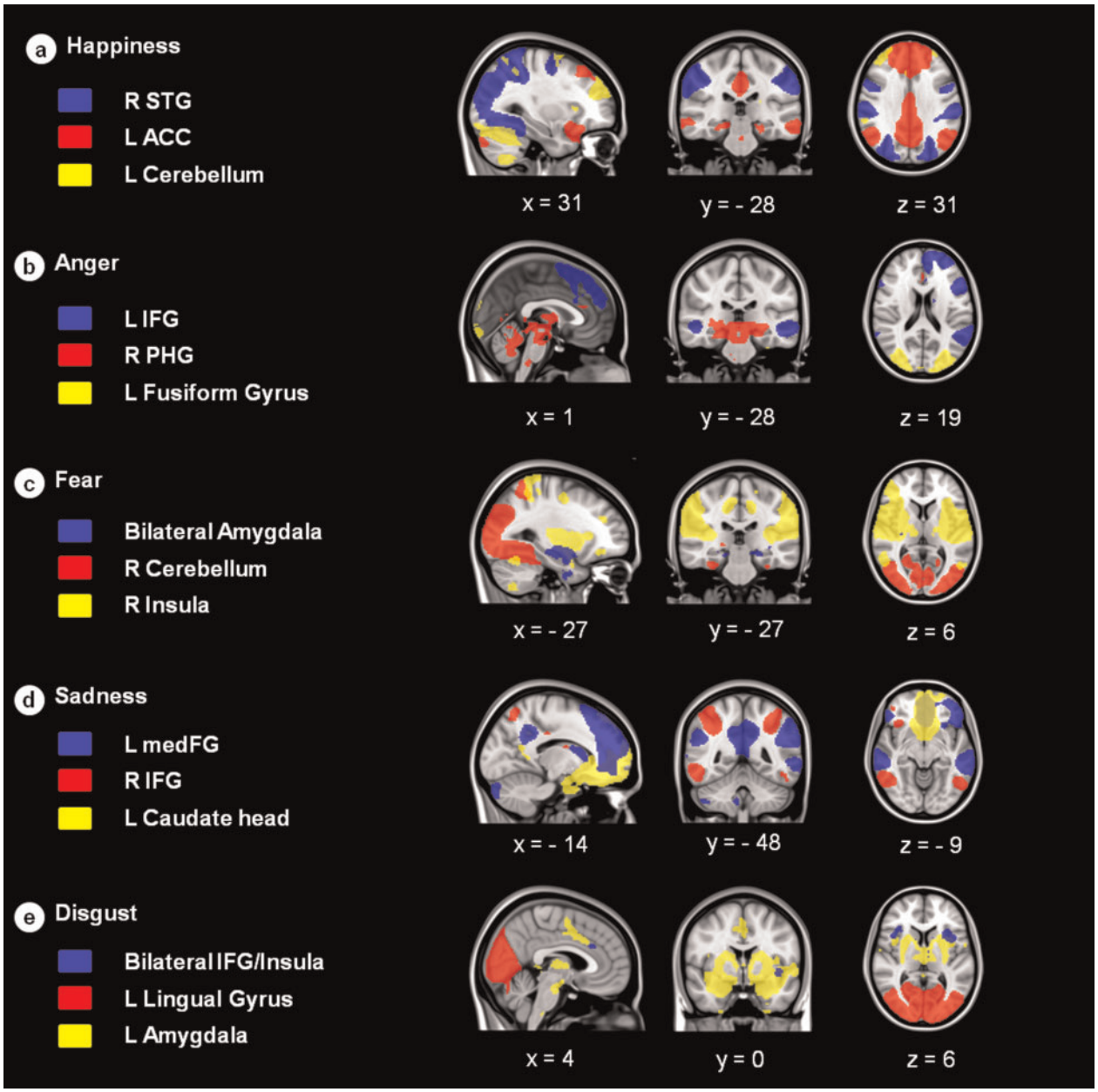

Fig. 1 The conjunction of discovery maps from meta-analytic activation peaks for happiness, anger, fear, sadness, and disgust at $z(r) = 0.1$ (Sample 1, $N = 89$). In **(a)**, voxels that preferentially correlate with the left superior temporal gyrus (STG) seed are shown in blue, voxels that correlate with left ACC seed are shown in red, and voxels that correlate with the left cerebellum seed are shown in yellow. In **(b)**, voxels that preferentially correlate with left inferior frontal gyrus (IFG) seed are shown in blue, voxels that correlate with right parahippocampal gyrus (PHG) seed are shown in red, and voxels that correlate with the fusiform gyrus seed are shown in yellow. In **(c)**, voxels that preferentially correlate with bilateral amygdala seed regions are shown in blue, voxels that correlate with the right cerebellum seed are shown in red, and voxels that correlate with right insula seed are shown in yellow. In **(d)**, voxels that preferentially correlate with left medial frontal gyrus (medFG) seed are shown in blue, voxels that correlate with the right inferior frontal gyrus (IFG) seed are shown in red, and voxels that correlate with the left caudate seed are shown in yellow. In **(e)**, voxels that preferentially correlate with bilateral inferior frontal gyrus/insula (IFG/insula) seed are shown in blue, voxels that correlate with the left lingual gyrus seed (IFG) are shown in red, and voxels that correlate with the left amygdala seed are shown in yellow. The binarized correlation maps, $z(r) = 0.1$ are overlaid on the 1 mm MNI152 T1-standard template image in FSL (http://www.fmrib.ox.ac.uk/fsl).

Supplementary Figure S4). Within each emotion category, the discovery maps did not show convergent overlap with just a single intrinsic network. For example, the superior temporal gyrus ROI that showed consistent increases in activity across studies of happiness was part of the visuospatial intrinsic network and the high-level visual network. In contrast, the left pregeneual ACC ROI that showed consistent increases across studies of happiness was part of the ventral salience network and dorsal DMN (see Table 3). Critically, intrinsic networks were identified in the discovery maps of multiple negative emotions categories. As an example, the domain-general dorsal salience network was identified in the discovery maps for different negative emotion categories, i.e. fear, disgust and sadness. The dorsal extent of the DMN was also identified in the discovery maps for all emotion categories (see Supplementary Figure S4).

Finally, as predicted by the conceptual act theory of emotion hypothesis, our seed and discovery method for the negative emotion categories revealed the salience network. Spatial overlap between discovery maps derived from the largest meta-analytic peak for each negative emotion revealed regions within the salience network, such ventral anterior insula, caudate and thalamus (Figure 3). To further

examine whether the ventral anterior insula, caudate and thalamus were indeed evidence of the broader salience network, we performed an exploratory analysis where we lowered the threshold to $z(r) = 0.05$. At this lower threshold, it became clear that the activity in ventral anterior insula, caudate and thalamus that we observed was indeed part of the canonical salience network (Seeley *et al.*, 2007; Touroutoglou *et al.*, 2012). Of note, we did not formally address whether seeds from happiness converged on the salience network, as there was only one positive emotion in our analysis. Nonetheless, as seen in the goodness-of-fit analysis (see Table 3), the happiness intrinsic connectivity map (anchored by the ACC) included regions that also overlapped with the ventral salience network.

Reliability of rs-fcMRI emotion maps

All networks showed high reliability across Samples 1 and 2, supporting the generalizability of our observations that basic emotion networks do not exist within the intrinsic architecture of the human brain. Most importantly, the ICC across the two samples for the connectivity $z(r)$ values between the trio of seeds associated with each emotion demonstrated high reliability for happiness (ICC = 0.98, two-way random effects, $p < 0.02$), fear (ICC = 0.98, two-way random effects, $p < 0.02$), sadness (ICC = 0.99, two-way random effects, $p < 0.09$) disgust (ICC = 0.99, two-way random effects, $p < 0.05$), although they were lower for anger (ICC = 0.65, two-way random effects, $p =$ ns).

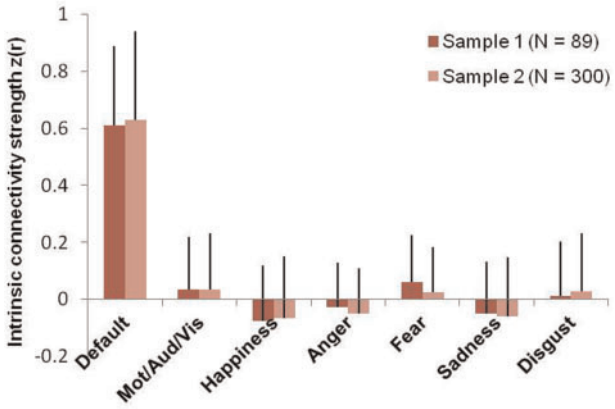

Fig. 2 The average strength of intrinsic connectivity, $z(r)$, values between the three seeds associated with each emotion category, the three seeds associated with the DNM (default mode network) (see Supplementary Materials), and the control seeds [associated with motor (Mot), auditory (Aud) and vision (Vis) networks; see Supplementary Materials] in Samples 1 and 2.

DISCUSSION

We used an intrinsic connectivity approach to compare two competing hypotheses about the brain basis of emotion. One view hypothesizes that certain emotions (anger, disgust, fear, happiness and sadness) are biologically 'basic' and arise from innate, anatomically constrained brain networks that are homologous in human and non-human animals. Support for this hypothesis would have arisen if we observed anatomically constrained intrinsic networks for specific emotions. This would have been observed if brain regions with consistent increases in activity during emotion experience and perception were each associated with a single intrinsic brain network (e.g. areas that had increased activity during experiences and perceptions of anger were part of an intrinsic network for anger). The alternative theoretical approach, the 'conceptual act theory' of emotion, hypothesizes that emotions are constructed from the interaction of domain-general, core systems within the brain. Support for the constructionist hypothesis would arise if we discovered that the regions consistently active during emotional experiences and perceptions were parts of domain-general networks that perform more basic psychological functions. The Vytal and Hamannn (2010) meta-analysis identified peak activation coordinates that consistently showed an increase in activation during the experience or perception of a given emotion spanning many studies using many different methods; we asked 'do the voxels in these peaks belong to the same intrinsic network in brain, or do they belong to different intrinsic networks working together?' Furthermore, the seed-based method employed here is sensitive enough to show spontaneous activity of subcortical regions (Bickart *et al.*, 2012). We therefore had the power to reveal evidence for anatomically based subcortical networks for each emotion that have been proposed by some basic emotion theorists (e.g. Panksepp, 1998), if they exist.

Using a 'seed and discovery' method, we did not find evidence for emotion-specific networks within the intrinsic functional architecture of the brain. Instead, our emotion discovery maps reflected combinations of domain-general networks, such as the salience network, DMN, basal ganglia network and executive control network, consistent with the hypothesis that different emotions arise from the interaction of domain-general systems within the brain (Barrett, 2012; Lindquist and Barrett, 2012; Barrett and Satpute, 2013). Further evidence for a domain-general constructionist account about emotion comes from our finding that a conjunction of discovery maps for anger, sadness, fear and disgust each revealed major nodes of the salience network

Table 3 The goodness-of-fit values for the emotion discovery maps

	Happiness			Anger			Fear				Sadness			Disgust			
Reference networks	R STG	L ACC	L cerebellum	L IFG	R PHG	L fusiform gyrus	L amygdala	R amygdala	R cerebellum	R insula	L medfg	R IFG	L caudate	R IFG/Insula	L IFG/Insula	L lingual gyrus	L amygdala
Dorsal salience										0.28		0.11		0.10			
Ventral salience		0.35		0.11							0.18						
Anterior salience				0.12						0.16							
Posterior salience										0.22							
Dorsal DMN		0.40									0.33		0.14				
Basal ganglia					0.11		0.12							0.19			0.11
Language				0.21													
L executive control											0.21						
Visuospatial	0.16											0.17					
Auditory										0.32							
Primary visual									0.12							0.31	
High-level visual	0.11					0.24			0.29							0.36	

Note: goodness-of-fit values lower than 0.1 are not shown in the table for ease of viewing.

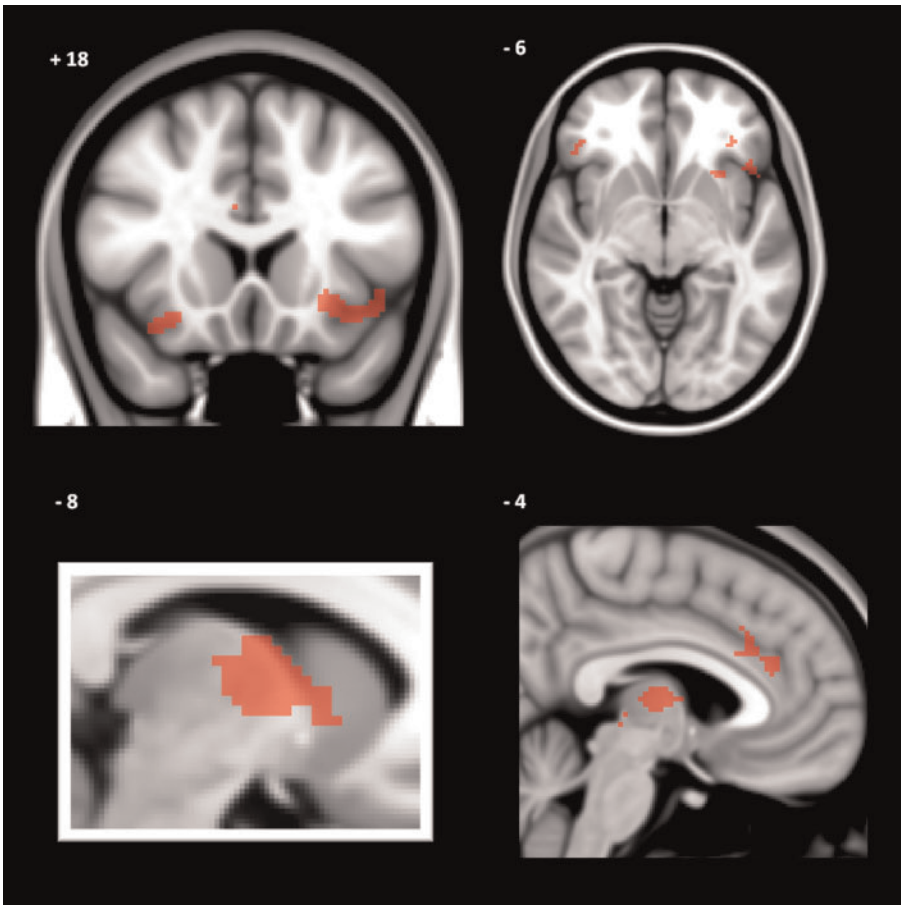

Fig. 3 A conjunction map for negative emotions. This figure displays a conjunction map of the binarized maps, $z(r) = 0.05$, seeded by the most prominent peak of each negative emotion (i.e., anger; L Inferior Frontal Gyrus seed, sadness; L medial Frontal Gyrus seed, fear; L amygdala seed, and disgust; L Inferior Frontal Gyrus/insula seed).

(Seeley *et al.*, 2007) consisting of the anterior insula, caudate, thalamus and ACC. Consistent with this interpretation, the salience network shows task-evoked activity during the experience of unpleasant affect (Hayes and Northoff, 2011; Lindquist *et al.*, 2015). Furthermore, individuals with stronger intrinsic connectivity in the salience network report more intense anxiety (Seeley *et al.*, 2007) and arousal when viewing negative images (Touroutoglou *et al.*, 2012). Our findings are also consistent with Laird *et al.* (2011)'s results showing that a limbic intrinsic connectivity system comprising mostly of limbic and medial temporal regions of the large-scale distributed salience network was associated with the perception of different emotions, i.e. happiness and fear. Together, these findings suggest that the salience network might be playing a general function across instances of anger, disgust, fear and sadness by representing the feeling of arousal that is common to each of the four emotion categories.

Using this interpretive framework, our results are consistent with other meta-analytic findings (Lindquist *et al.*, 2012) showing that many of the brain regions with consistent increases in activation across studies of the same emotion category are, in fact, nodes from different intrinsic networks that have been associated with other basic psychological functions, such as attention, language, memory, salience detection and motor control. Moreover, brain regions with consistent increases during emotion experience and perception can be decomposed into a set of functional groups (i.e. regions that coactivate across studies) (Kober *et al.*, 2008) that resemble the intrinsic networks we observed in the present report. One possibility then is that intrinsic networks support general psychological processes that form fundamental 'ingredients' that contribute to the construction of all manner of mental states (Lindquist and Barrett, 2012; Barrett and Satpute, 2013). For instance, the salience network appears to play a general function across instances of anger, disgust, fear and sadness (Lindquist *et al.*, 2012) as well as other 'emotional' events including empathy (Decety and Jackson, 2004) and autonomic regulation (Craig, 2002; Vogt, 2005). Nodes within the 'salience' network are also engaged during 'cognitive' events, such as language and executive function tasks [i.e. dorsal anterior insula and dorsal ACC; (Nelson *et al.*, 2010; Touroutoglou *et al.*, 2012)] and attention allocation tasks [i.e. dorsal anterior insula and dorsal ACC; (Corbetta *et al.*, 2008)]. This lack of domain-specificity has led to the interpretation that the salience network functions to orient the brain's processing capacity toward the most homeostatically relevant information (constituting a body-based source of attention within the human brain; Lindquist and Barrett, 2012; Barrett and Satpute, 2013) to guide the brain's 'switching' or 'reorienting' between 'internal' and 'external' events (Corbetta *et al.*, 2008; Menon and Uddin, 2010).

Similarly, nodes within the DMN are engaged during emotion (Lindquist *et al.*, 2012), and also appear to serve more domain-general functions. The DMN nodes are engaged in remembering personal events (autobiographical memory) (Buckner *et al.*, 2008), imagining the future (prospection) (Andrews-Hanna *et al.*, 2010), accessing memory for word meanings (semantic memory), scene construction and context-based object perception (Binder *et al.*, 2009) as well as moral reasoning (Bzdok *et al.*, 2012) and person perception, leading to the suggestion that the DMN creates 'situated conceptualizations'

(Barrett, 2012; Lindquist *et al.*, 2012; Lindquist and Barrett, 2012) or 'mental models' (Barrett and Satpute, 2013) of the meaning of sensations from the body and world during cognitions, emotions and perceptions.

It is tempting to assume that the lack of specificity for each emotion category is a function of the coarse spatial and temporal resolution in the resting-state brain data (or the brain imaging experiments, for that matter), but even human lesion studies (Hurlemann *et al.*, 2009; Feinstein *et al.*, 2013) and studies that electrically stimulate specific neurons in fully conscious humans have not been able to identify specific neural modules for specific emotions [e.g. (Guillory and Bujarski, 2014); for a review of studies, see (Barrett *et al.*, 2007)]. For instance, consistent with our intrinsic network findings, electrical stimulation of the human brain from intracranial electrodes reveals broadly distributed networks across the cortex, paralimbic and limbic cortex and subcortex that contribute to the representation of multiple emotional states (Guillory and Bujarski, 2014). A growing evidence from other domains has also failed to find evidence of biologically basic emotions, such as studies of autonomic function in humans (Cacioppo *et al.*, 2000; Kreibig, 2010), facial expressions in infants and adults (Camras *et al.*, 2002; Russell *et al.*, 2003; Barrett and Kensinger, 2010; Barrett, 2011) and studies of vocal acoustics (Bachorowski and Owren, 2002).

A related possibility is that emotions are represented as task-evoked functional brain networks that flexibly combine in a given moment to produce the experience or perception of anger, disgust, fear, happiness, sadness and so on [as hypothesized (Hamann, 2012)]. Such a hypothesis is not orthogonal to a constructionist interpretation we are offering, although we did not examine task-dependent BOLD data and so did not test this idea explicitly in this report. For example, if the brain possesses of a set of intrinsic networks that can be understood as performing domain-general operations, then it is possible that each process can be observed as a set of basic processing modes [aka 'functional motifs' (Sporns and Kotter, 2004)], arising from the anatomical connections that undergirds each network [aka 'structural motifs' (Sporns and Kotter, 2004)]. In this framework, individual instances of anger, disgust, fear, etc, could be understood as high dimensional brain states reflecting neural assemblies within broadly distributed networks, as well as the dynamic interaction of those assemblies (cf. Lindquist and Barrett, 2012; Barrett and Satpute, 2013). Consistent with this prediction, in another study from our lab we used task-evoked functional connectivity and examined the relationship between the intensity of ongoing emotional experiences of anger, sadness and fear, on the one hand, and the continually fluctuating functional connectivity strength between regions of the salience and default networks on the other (Raz, Touroutoglou *et al.*, under review). Across five samples of subjects, we predicted and found that the dynamic variation in the functional connectivity between intrinsic networks across time (i.e. changing cohesiveness) constituted a shared mechanism for intense experiences of sadness, fear and anger. These findings are ultimately consistent with the findings reported herein because they suggest that momentary experiences of emotion are related to the functional coupling of intrinsic connectivity networks.

More broadly, our findings are consistent with an alternative framework for understanding the brain's functional architecture. The fact that peak activations from different emotion categories belong to domain-general intrinsic functional connectivity networks is consistent with a broader constructionist view of the mind (Lindquist and Barrett, 2012; Barrett and Satpute, 2013), more generally. A constructionist model of mind–brain correspondence hypothesizes that all mental states emerge (i.e. are 'constructed') from the interaction of more basic psychological processes that are not specific to folk psychological distinctions such as 'emotion', 'cognition', 'memory' or 'perception'. Emotions, cognitive functions and perceptions can be thought of as mental events (prompted by specific experimental tasks or arising as naturally occurring states) that are constructed from interactions within and between intrinsic networks that compute domain-general functions. A host of neuroscience research findings point toward a constructionist functional architecture of the brain that relies on distributed structure-function mappings. This constructionist approach echoes other debates about modularity throughout neuroscience (e.g. in face perception), which center on whether a phenomenon has dedicated neural modules or is constructed from more domain-general elements (Anderson and Finlay, 2014; Grill-Spector and Weiner, 2014). Taken together, our and other findings stress the need for revisions in the psychological ontologies so that they are consistent with structure and function of the brain [cf. (Poldrack, 2010; Fox and Friston, 2012; Lindquist and Barrett, 2012; Anderson *et al.*, 2013; Barrett and Satpute, 2013)].

SUPPLEMENTARY DATA

Supplementary data are available at *SCAN* online.

Conflict of Interest

None declared.

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