UNSUPERVISED CLASSIFICATION REVEALS DEGENERATE NEURAL REPRESENTATIONS OF EMOTION

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ABSTRACT

Cameron M. Doyle: Unsupervised classification reveals degenerate neural representations of emotion
(Under the direction of Kristen A. Lindquist)

Neural degeneracy refers to the idea that distinct neural systems are capable of performing the same functions (Noppeney, Friston, & Price, 2004). Consistent with neural degeneracy, the Theory of Constructed Emotion (TCE) suggests that emotions and other mental states arise from combinations of the brain's domain-general intrinsic networks such as the default mode network, salience network, and frontoparietal control network (Clark-Polner, Johnson, & Barrett, 2017). A key prediction of degeneracy and the TCE is that the same emotion can emerge from distinct patterns of connectivity across time or across individuals (Barrett, 2017). This project specifically investigates the principle of neural degeneracy in emotion for the first time using a data-driven model building algorithm with unsupervised classification (S-GIMME; Gates, Lane, Varangis, Giovanello, & Guskiewicz, 2017) to quantify distinct patterns of between-network connectivity during self-generated experiences of anxiety and anger. Twenty-four subjects underwent an fMRI experiment in which they listened to unpleasant music and self-generated experiences of anxiety and anger. The hypotheses of this experiment were tested in four consecutive analysis steps. The first analysis step revealed that the S-GIMME procedure could roughly reproduce the experimental conditions in the present experiment by subgrouping individuals based on patterns of connectivity that differentiated anger and anxiety. The second analysis step revealed that this variation could be further subdivided into degenerate neural pathways within each emotion category. The third analysis step showed that subgroups

revealed during the anger and anxiety conditions are distinct from those found during a task-positive control condition in which participants listened to neutral music but did not generate an emotional experience. Finally, the fourth analysis step provided a more stringent test of the degeneracy hypothesis by showing that distinct patterns of connectivity revealed in the previous analyses are not the result of stable individual differences that would also be present at rest. Taken together, these analyses show that different patterns of connectivity are associated with the experience of the same emotion.

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LIST OF ABBREVIATIONS

aSAL	Anterior Salience Network
BG	Basal Ganglia Network
DAN	Dorsal Attention Network
dDMN	Dorsal Default Mode Network
Lang	Language Network
lFPC	Left Frontoparietal Control Network
PCUN	Precuneus Network
pSAL	Posterior Salience Network
rFPC	Right Frontoparietal Control Network
SMN	Sensorimotor Network
vDMN	Ventral Default Mode Network

CHAPTER 1: BACKGROUND

Degeneracy refers to the ability of distinct biological mechanisms to produce the same outcomes (Edelman & Gally, 2001; Tononi, Sporns, & Edelman, 1999). The principle of degeneracy is well-documented within biological systems (see Edelman & Gally, 2001 for multiple examples). For instance, degeneracy is present in the genetic code, where 64 codon triplets code for only 20 different amino acids (Shu, 2017). Degeneracy is also present in the immune system, where many different antigens can bind to a single type of T-cell to produce the same immune response (Eisen, 2001). Degeneracy even appears in cognition, where structurally distinct sentences can communicate the same message (Edelman & Gally, 2001), and distinct acoustic outputs are understood to have the same meaning (e.g., when the phonetic form of a word is distorted by noise or speaker variability; Winter, 2014). Relatively less studied, however, is how degenerate mechanisms in the brain can produce the same outcome. This work examines, for the first time, how degenerate neural network patterns produce experiences of anger and anxiety.

Degeneracy in the brain

A small body of work has shown that in the brain, distinct neural systems can perform the same functions. For example, in rodents, different subsets of neurons in medial prefrontal cortex code for the same social exploration behavior (Liang et al., 2018). Similarly, degenerate ensembles of neurons can produce the same defensive behavior based on the context the organism is in (Barrett & Finlay, 2018). In healthy humans, two distinct neural pathways are associated with reading aloud familiar words. Whereas some participants appear to rely more on

left inferior frontal and anterior occipito-temporal regions, others rely on right inferior parietal and left posterior occipito-temporal regions when reading aloud the same familiar words (Seghier, Lee, Schofield, Ellis, & Price, 2008).

Degeneracy likely exists because it makes complex systems more robust to insult (Sporns, Tononi, & Edelman, 2000; Tononi et al., 1999; Whitacre & Bender, 2010). For instance, degeneracy explains how human lesion studies can reveal preserved emotional functioning despite destruction of brain regions (e.g., limbic structures) that are strongly linked to emotional function (Becker et al., 2012; Damasio, Damasio, & Tranel, 2013; Feinstein, 2013; Feinstein et al., 2016, 2010). Indeed, bilateral amygdala lesions following Urbach-Wiethe disease caused vastly different emotional outcomes in one set of identical twins. Whereas one twin has impaired fear perception and startle response following amygdala lesions (consistent with findings in the broader literature; Adolphs, Tranel, Damasio, & Damasio, 1994, 1995; Bach, Hurlemann, & Dolan, 2015; Siebert, Markowitsch, & Bartel, 2003), the other has a preserved ability to perceive fear on faces and exhibits an intact startle response (Becker et al., 2012). One twin appears to require functioning amygdalae for fear-related responses, whereas the other does not. Another study showed that different brain networks mediate performance on a memory task in patients with Alzheimer's Disease (AD). Most AD patients showed recruitment of a network involving left posterior temporal cortex, calcarine cortex, posterior cingulate, and the cerebellar vermis. However, a subset of patients showed recruitment of a network involving the left anterior cingulate and the anterior insula, a pattern shared with healthy controls (Stern et al., 2000).

Despite its prevalence in biological systems, however, degeneracy has traditionally been under-studied in neuroscience (Mason, Domínguez, Winter, & Grignolio, 2015). It is possible that degeneracy is a relatively neglected topic of neuroscientific inquiry because it is

fundamentally at odds with traditional confirmatory approaches, which seek to find the specific brain region(s) or network(s) responsible for a certain outcome (De Schutter, 2016). These confirmatory approaches tend to assume that each brain region or network serves a mutually exclusive function and that the hypothesized structure-function mapping is invariant across instances of measurement. In human research, these assumptions were to date reaffirmed by the type of data collected. For instance, human lesion studies traditionally relied on dissociations of brain structure and function (e.g., showing that amygdala lesions produced fear deficits, but not deficits in other emotions; Adolphs, Tranel, Damasio, & Damasio, 1995; Feinstein, Adolphs, Damasio, & Tranel, 2011). Similarly, univariate neuroimaging analyses used experimental contrasts to reveal mean-level activation in isolated brain regions, giving the impression that certain regions responded to one construct and only one construct.

Although important in their own right, such confirmatory approaches may obscure the degeneracy inherent in complex systems. Studies that perform interindividual analyses to find mean-level responses assume that mean-level responses describe the processes inherent in the population, more broadly. Yet it is often the case that mean-level responses do not describe any single participant's response in the sample from which they were derived (Molenaar & Campbell, 2009). In neuroscience, there is substantial heterogeneity in terms of which brain regions are active across different subjects during the same task (Eisenberger, Gable, & Lieberman, 2007; Hester, Fassbender, & Garavan, 2004; Ojemann, Ojemann, Lettich, & Berger, 2008; Tavor et al., 2016; Wager, Jonides, Smith, & Nichols, 2005; for reviews see Miller & Van Horn, 2007; van Horn, Grafton, & Miller, 2008) and how those regions are connected to one another (Elliot et al., 2019; Feilong, Nastase, Guntupalli, & Haxby, 2018; Gratton et al., 2018; Mueller et al., 2013; Vanderwal et al., 2017). A drawback of performing group-level analyses on

these types of data is that spurious findings can arise (see Gates & Molenaar, 2012). The study of emotion is no exception, where it is frequently assumed that a single emotion category (e.g., anxiety) is associated with a single anatomically-defined neural circuit in non-human animals (Izard, 2007; Panksepp, 1982; 2011) and that mean-level brain activity as measured by fMRI in humans reflects activity within that singular circuit.

Degeneracy in the brain basis of emotion

The idea that experiences of a certain type of emotion category emerge from a singular neural pattern is typified in the classical view of emotion, which argues that each emotion derives consistently from a specific neural structure (Ekman, 1992; Panksepp, 1982; Panksepp & Watt, 2011). In its most modular form, the classical view proposes that fear is associated with the amygdala (e.g., Bechara et al., 1995; LaBar, Gatenby, Gore, LeDoux, & Phelps, 1998), disgust with the anterior insula (e.g., Jabbi, Bastiaansen, & Keysers, 2008; Wicker et al., 2003), anger with orbitofrontal cortex (e.g., Harmon-Jones & Sigelman, 2001; Harmon-Jones & Allen, 1998; Murphy, Nimmo-Smith, & Lawrence, 2003; Vytal & Hamann, 2010), and sadness with anterior cingulate cortex (e.g., Murphy et al., 2003; Phan, Wager, Taylor, & Liberzon, 2002). However, much evidence calls the classical view into question. Studies of patients with intractable epilepsy reveal that intracranial stimulation of several different brain regions (e.g., amygdala, insula, parahippocampal gyrus) can produce the same emotional experience (i.e., fear), suggesting that there is not a one-to-one mapping of fear to the amygdala (Guillory & Bujarski, 2014). Meta-analyses of the human neuroimaging literature also fail to find a consistent and specific link between emotion categories such as anger, fear, sadness, disgust, or happiness and any single anatomically-defined brain region (e.g., fear is not uniquely associated with amygdala activation) (Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012; Vytal & Hamann, 2010). Nor are

there consistent and specific associations between emotion categories and anatomically-defined brain networks (Touroutoglou, Lindquist, Dickerson, & Barrett, 2015).

Without evidence for consistent and specific mapping of brain regions or networks to emotion categories, researchers turned to multivariate tools to attempt to map emotions to distributed patterns across large-scale brain networks (Kragel & LaBar, 2016). Studies using such techniques (e.g., multi-voxel pattern analysis; MVPA) to classify neural patterns associated with certain emotion categories can identify patterns associated with experiencing one emotion category (e.g., fear) v. another (e.g., anger) at levels greater than chance. However, these patterns span the cortex and subcortex and fail to satisfy a critical assumption of the classical view. Namely, these studies have been unable to show that the "neural signature" for a given emotion is the same across all instances (Saarimäki et al., 2016; see Clark-Polner et al., 2017 for a discussion), and purported neural signatures do not replicate across pattern classification studies (e.g., Kassam, Markey, Cherkassky, Loewenstein, & Just, 2013; Kragel & LaBar, 2015; Saarimäki et al., 2016; see Barrett, 2017). Moreover, MVPA does not reveal anatomical structures that are unique to specific emotions, but rather patterns of functional brain activation within arbitrarily defined voxels that span neural networks involved in a host of basic functions such as visceromotor control, cognitive control, the representation of body states, and the representation of features of the situation (Wager et al., 2015).

Thus, in contrast to the classical view of emotion, the evidence is more consistent with the constructionist systems neuroscience hypothesis that emotions are represented as complex interactions between brain regions that support more basic psychological processes that are not themselves unique to emotions. For instance, meta-analyses (Alcalá-López et al., 2018; Kober et al., 2008; Wager et al., 2015) as well as individual studies (Brooks et al., *under revision*; Raz et

al., 2016, 2012) find that emotional experiences such as anger and fear are associated with connectivity within and between the brain's intrinsic neural networks. In a meta-analysis of 148 studies, Wager et al. (2015) found that anger was characterized by coactivation between visual and frontoparietal areas, between cortical areas and the cerebellum and amygdala, within frontoparietal and dorsal attention networks, and within subcortical structures. Fear was associated with strong basal ganglia coactivation with the amygdala and thalamus, as well as weak cortical-subcortical coactivation and weak intracortical coactivation. I take this work one step further by examining degeneracy in the connectivity between these networks within a sample of individuals during anger and anxiety.

CHAPTER 2: METHOD

Whereas confirmatory approaches tend to analyze the role of specific neural regions or networks in emotion, I relied on a data-driven method to reveal differences in neural pathways during emotion experience. Prior work has examined individual differences in psychological experience and their corresponding neural correlates, but those studies tend to investigate differences in the degree to which the same neural correlate of a phenomenon is activated between people. For example, amygdala and prefrontal connectivity is associated with individual differences in spontaneous use of emotion regulation techniques (Drabant, McRae, Manuck, Hariri, & Gross, 2009), as well as individual differences in rumination when participants are instructed to increase or decrease negative affect (Ray et al., 2005). In addition to the possibility of the same regions showing differential connectivity between individuals, degeneracy argues that different neural regions and networks could be involved in the experience of the same emotion category across individuals (Noppeney et al., 2004). In the present research, I conducted four analyses to test the hypothesis that distinct neural networks can produce the same category of emotional experience across individuals. I employed existing data from an fMRI experiment in which participants completed a resting state scan, followed by scans in which experiences of anger, anxiety, and a neutral state were evoked using the continuous music technique (Eich, Macaulay, & Ryan, 1994; Eich & Metcalfe, 1989). To conduct these analyses, I used a data-driven model selection algorithm that identifies subgroups of individuals with different connectivity maps (Subgrouping-Group Iterative Multiple Model Estimation; Gates et al., 2017). The original GIMME algorithm (Gates & Molenaar, 2012) was developed as a method for

arriving at robust individual-level models of directed brain connectivity (i.e., networks) using the unified structural equation modeling (uSEM; Kim, Zhu, Chang, Bentler, & Ernst, 2007) framework. GIMME first seeks to identify group-level patterns of activation that are shared across the majority of individuals, and then uses group-level paths as priors for an individual-level search. Simulations have shown that this process improves the recovery of individual-level paths (Gates & Molenaar, 2012). The subgrouping GIMME (S-GIMME) algorithm builds on the original GIMME algorithm by identifying subgroups of individuals with similar patterns of activation.

The S-GIMME algorithm is especially well-suited for investigating degeneracy in emotion because it not only arrives at robust individual-level models characterizing patterns of activation, but it can also identify subgroups of individuals who have similar patterns of activation. This procedure represents a unique advantage over traditional approaches, which often discard individual differences in neural network activity as random noise (Dubois & Adolphs, 2016; Kanai & Rees, 2011; Molenaar, 2004; Seghier & Price, 2018). See Gates et al. (2017) and Lane, Gates, Pike, Beltz, & Wright (2018) for full details documenting the performance and finite sampling behavior of the S-GIMME algorithm. Discovering subgroups of individuals who differ in their patterns of neural activation during the same emotional experience would provide evidence for degeneracy in the brain basis of emotion.

My approach is ultimately exploratory, but I nonetheless had *a priori* hypotheses about the neural networks that would be involved in anger and anxiety and the features of experience they might correspond to. For instance, based on prior research (e.g., Kober et al., 2008; Wager et al., 2015), I predicted that emotion experience would be characterized by distributed activity within and between a set of intrinsic networks including the default mode network (DMN), the

frontoparietal control network (FPC), the salience network (SAL), and the dorsal attention network (DAN). See Table 1 for a list of intrinsic networks and the cognitive processes with which they are associated.

Table 1. Intrinsic networks of interest and their general functions.

Network	Functions
Default Mode (DMN)	Self-referential thought, autobiographical memory, mentalization (Buckner, Andrews-Hanna, & Schacter, 2008).
Frontoparietal Control (FPC)	Cognitive control (Dosenbach et al., 2007), decision-making (Vincent, Kahn, Snyder, Raichle, & Buckner, 2008).
Salience (SAL)	Represents cognitive, homeostatic, or emotional salience (Seeley et al., 2007).
Dorsal Attention (DAN)	Voluntary direction of attention towards environmental stimuli (Corbetta & Shulman, 2002; Fox, Corbetta, Snyder, Vincent, & Raichle, 2006; Vossel, Geng, & Fink, 2014)

Note: this list of networks and functions should not be considered comprehensive. There are more intrinsic networks than those listed, and each network likely plays a role in myriad functions other than those listed.

In analysis 1, I assessed whether distinct emotional experiences could be identified based on patterns of brain connectivity. Consistent with my predictions, I found that the S-GIMME procedure roughly reproduced the experimental conditions in the present experiment on the basis of participants' brain connectivity. In analysis 2, I assessed the possibility of degeneracy in the distributed patterns of brain activation within the experience of anger and anxiety. I predicted and found that some aspects of connectivity patterns were shared by subsets of the sample, and that those subsets could be identified through an unsupervised classification search. Although the subgroups did not experience categorically distinct emotional states, they experienced differences in the phenomenological features associated with those states (e.g., how intense v. unpleasant v. activated an experience of anger is). These findings suggest degeneracy in the patterns of neural activation during the same emotional experience. However, it remains possible that the observed subgroups reflect person-level factors and are not a specific product of the

evoked anger and anxiety states. To rule out this alternate explanation, I conducted two additional analyses. In analysis 3, I implemented the subgrouping procedure on the neutral music condition to assess whether the same subgroups might be revealed during a task-positive control condition in which participants listened to neutral music but did not generate an emotional experience. I predicted and found that subgroups revealed during the neutral condition did not correspond to the subgroups revealed during the emotion induction conditions. In analysis 4, I tested whether the subgroups revealed in previous conditions might also be present at rest, which would suggest that the classification procedure used in the present study is selecting on individual differences unrelated to the experience of emotion or any other task-based state. I predicted and found that the brain states revealed during rest were consistent with typical resting state functional connectivity patterns, and that these patterns were distinct from those revealed during the previous conditions.

Participants. Twenty-four adults (13 female, M_{age} = 22.92, SD_{age} = 4.95) were recruited from the community to participate in a neuroimaging study on "music and the brain." Participants were healthy, right-handed, and had no MRI contraindications or history of psychiatric illness. All participants had normal hearing and wore MRI-compatible headphones during their scans. Participants provided informed consent and were financially compensated in a manner jointly approved by the Institutional Review Boards at The University of North Carolina at Chapel Hill and The University of North Carolina at Greensboro.

MRI Acquisition. Participants were scanned on a 3T Siemens Magnetom Trio at the Joint School for Nanoscience and Nanoengineering at The University of North Carolina at Greensboro. Structural images were acquired using a 3D MPRAGE T1-weighted sequence with the following parameters: TR = 2530ms, TE = 2.26ms, voxel size = 1.0 mm^3. Functional images

were collected using a single-shot gradient-echo echo-planar imaging sequence with a TR of 2000ms, a TE of 30ms, and a voxel size of 3.1 x 3.1 x 4.0 mm.

Procedure

The continuous music technique (CMT; Eich, Macaulay, & Ryan, 1994; Eich & Metcalfe, 1989) was used to induce emotion in the scanner. In a typical CMT paradigm, participants listen to emotionally evocative music while recalling or imagining emotional events. The CMT has been shown to successfully induce stable and substantial changes in participants' moods (Eich, 1995). Participants completed six runs in a single fMRI session. Participants first completed a resting state scan, followed by a neutral music run, where they simply listened to neutral music with no specific instructions, and a negative music run, where they listened to a piece of music intended to induce unspecified negative affect. During the negative music run, participants were not given any specific instructions to generate a negative emotional experience. Next, participants listened to the same negative music and were asked to self-generate an experience of either anger or anxiety (order was counterbalanced across participants). Participants then completed a second negative music run where they listened to a different piece of negative music without specific instructions. Finally, participants listened to that second piece of negative music again and generated an experience of the other discrete emotion (i.e., if they generated an experience of anger in run 4, they generated an experience of anxiety in run 6). Each run lasted 5 minutes, for a total of 30 minutes of scan time.

For each emotion induction run, participants listened to either Holst's *The Planets* or Beethoven's *Gross Fugue Op. 133 in B Flat*. As in prior work (e.g., Eich, Macaulay, & Ryan, 1994; Eich & Metcalfe, 1989; Lindquist & Barrett, 2008), compositions were selected to induce negative, high arousal affect. Run order and emotion-music pairing were counterbalanced across

participants. For example, some participants were randomly assigned to generate a feeling of anger while listening to *The Planets* and a feeling of anxiety while listening to *Gross Fugue Op. 133 in B Flat*, and other participants were randomly assigned to generate a feeling of anxiety while listening to *The Planets* and a feeling of anger while listening to *Gross Fugue Op. 133 in B Flat.* The present analyses focus on the resting state, neutral music, and specific anger and anxiety conditions during which participants were asked to generate an experience of anger or anxiety, respectively. I provide additional information on those conditions below.

Resting state. Participants completed a resting state scan, which served as a task-neutral control condition. Participants viewed a blank screen and were told to "keep [their] eyes open and [their] mind at rest."

Neutral music. Participants listened to an instrumental piece called *A New Day Has Come* by the pianist and composer George Skaroulis. A collaborator and classically trained musician selected this piece for the neutral music run because it is as affectively neutral as possible based on key and beats per minute. Participants viewed a blank screen and were told to "listen to the music and maintain a calm and neutral state throughout."

Negative music 1 and anger induction. Participants listened to one of the counterbalanced selections of unpleasant music and were asked to self-generate an experience of anger by drawing on prior experiences or visualizing imaginary experiences. They were told "this piece has been shown to make people feel very angry. Cultivate a feeling of anger in response to it."

Negative music 2 and anxiety induction. Participants listened to the other counterbalanced selection of unpleasant music and were asked to self-generate an experience of anxiety by drawing on prior experiences or visualizing imaginary experiences. They were told

"this piece has been shown to make people feel very anxious. Cultivate a feeling of anxiety in response to it."

Measures. During breaks between runs, participants used a visual analog scale (VAS) to rate the extent to which they felt unpleasant, activated, anxious, and angry during the previous run. Rating options ranged continuously from 0 (not at all) to 10 (extremely). Following the entire scanning procedure, participants completed a series of questionnaires and reported on what they chose to imagine to evoke emotional experiences while in the scanner. Questionnaires included the Range and Differentiation of Emotional Experiences Scale (RDEES; Kang & Shaver, 2004) and the Twenty-Item Toronto Alexithymia Scale (TAS-20; Bagby, Parker, & Taylor, 1994). The RDEES includes 14 items designed to assess individual differences in emotional complexity. The scale is composed of two subscales measuring 1) range and 2) differentiation of emotional experience. The range subscale assesses the span of different emotions experienced by an individual, and the differentiation subscale assesses how well an individual distinguishes between "similar" emotions (Kang & Shaver, 2004). The TAS-20 includes 20 items designed to measure Alexithymia, a subclinical condition marked by the inability to characterize one's own emotions (Parker, Taylor, & Bagby, 1989; Sifneos, 1973). The TAS-20 is divided into three subscales assessing 1) Difficulty Identifying Feelings, 2) Difficulty Describing Feelings, and 3) Externally Oriented Thinking. I reasoned that the RDEES and TAS-20 measures would capture individual differences in the complexity and quality of people's daily emotional experiences, which may relate to how they self-generated emotions in the scanner.

Finally, participants were asked to report what they chose to imagine while generating emotional experiences in the scanner. The self-report data were coded based on presence and

frequency of certain words in participants' reports. Coded information included the frequency of emotion words (e.g., "anger"), frequency of valence words (e.g., "unpleasant"), frequency of arousal words (e.g., "activated"), and frequency of body state words (e.g., "sweating"). In addition, participants' self-reports were coded for the extent to which they were internally or externally focused, the extent to which they included social or non-social content, and whether they reported autobiographical or prospective scenarios (scored on 1-7 Likert scales).

Data Preparation

Preprocessing. Data were preprocessed using the CONN functional connectivity toolbox (Whitfield-Gabrieli & Nieto-Castanon, 2012), which implements preprocessing steps from SPM12. Functional data were realigned and unwarped, slice-timing corrected, examined for excessive motion using the Artifact Detection Tools (ART) toolbox (https://www.nitrc.org/projects/artifact_detect/), co-registered to structural images, normalized to MNI space, and spatially smoothed using an 8mm FWHM Gaussian kernel. Rather than using global signal regression, which may potentially induce spurious negative correlations among intrinsic networks (Murphy, Birn, Handwerker, Jones, & Bandettini, 2009), functional data were denoised using the CompCor toolbox (Behzadi, Restom, Liau, & Liu, 2007). CompCor is a components-based correction method which regresses signal from five principal components of white matter and cerebrospinal fluid, rather than the average signal from all voxels in the brain. This method circumvents the issue of potentially inducing artefactual negative correlations while still removing noise from white matter and CSF voxels.

Time Series Extraction. In addition to implementing a standard SPM12 preprocessing pipeline, I used the CONN toolbox to extract time series from ninety ROIs within fourteen intrinsic functional networks (Shirer, Ryali, Rykhlevskaia, Menon, & Greicius, 2012) for

network-based analyses within S-GIMME. I uploaded ROI masks for each of the ninety ROIs in the Shirer et al. (2012) parcellation prior to preprocessing the data in CONN. Upon completion of the preprocessing steps, CONN produced a data file for each participant containing the denoised time series for each of the uploaded ROIs. Thus, each participant's data file contained 150 time points per condition for each of the 90 ROIs in the Shirer et al. (2012) parcellation. Whereas most applications of GIMME or S-GIMME examine connectivity between ROIs forming hubs within a single network (Gates, Molenaar, Iyer, Nigg, & Fair, 2014; McCormick & Telzer, 2018) or ROIs distributed across several networks (McCormick, Gates, & Telzer, 2019; Yang, Gates, Molenaar, & Li, 2015; Zelle, Gates, Fiez, Sayette, & Wilson, 2017), the present application is novel in that it performs data reduction of ROIs to examine connectivity between entire networks. GIMME is based in a structural equation modeling (SEM) framework, which requires a large sample size (here, a large number of time points) relative to the number of parameters to be estimated (Bentler & Chou, 1987). Further, the algorithm employs a computationally intensive iterative process for arriving at group-, subgroup-, and individual-level connectivity maps. Thus, data reduction was required to improve the feasibility of between-network analyses, from both a modeling and a computational perspective.

Network Selection. As a first step in reducing the number of parameters to be estimated, I excluded 3 primary sensory networks from the Shirer et al. (2012) parcellation that were less critical to the present study (i.e., auditory, primary visual, and high visual networks). Including these networks would be an interesting avenue for future research, as I would expect to see differences in sensory involvement across emotion categories, as well as across individuals. However, such differences in these networks are less likely to meaningfully correspond to the phenomenological features of participants' emotional experiences, which are the focus of the

present study. Thus, the present analyses were conducted on the 11 remaining functional networks in the Shirer et al. (2012) parcellation.

Several of the Shirer et al. functional networks are subnetworks of broader intrinsic networks. It is well-known in the literature that intrinsic networks can be combined or decomposed to form either broader networks or more granular subnetworks (Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010; Dixon et al., 2018; Hyatt, Calhoun, Pearlson, & Assaf, 2015; Yeo et al., 2011). The ways in which networks fractionate into subnetworks tends to replicate across the literature. I thus opted to analyze the more granular parcellation of the functional networks described in Shirer et al. (2012) with the hope of revealing more heterogeneity across individuals.

I included the Shirer et al. (2012) dorsal and ventral default mode subnetworks (dDMN and vDMN, respectively), which together comprise the canonical default mode network (Greicius, Krasnow, Reiss, & Menon, 2003; Raichle, 2015; Raichle et al., 2001). I also examined the anterior and posterior salience subnetworks (aSAL and pSAL, respectively) which comprise the canonical salience network (Seeley et al., 2007). I examined the Shirer et al. (2012) left and right executive control networks (LECN and RECN, respectively), which together comprise the canonical frontoparietal control network (FPC; Dosenbach et al., 2007; Fair et al., 2007, hereafter referred to as lFPC and rFPC). I also examined Shirer et al.'s (2012) visuospatial network, referred to here and elsewhere as the dorsal attention network (DAN; Corbetta & Shulman, 2002; Fox, Corbetta, Snyder, Vincent, & Raichle, 2006; Vossel, Geng, & Fink, 2014).

In addition to these more canonical intrinsic networks, I examined the language network (Lang), which includes brain regions responsible for language production and comprehension (Tomasi & Volkow, 2012), because access to semantic emotion concepts (e.g., the word "anger")

contributes to experiences of emotion (Brooks et al., 2017; Lindquist, MacCormack, & Shablack, 2015). I examined the sensorimotor network (SMN) because emotion potentiates motor action (Hajcak et al., 2007), and the basal ganglia (BG) because recent evidence has implicated these subcortical nuclei in various cognitive and affective processes (Arsalidou, Duerden, & Taylor, 2013). Finally, I examined Shirer et al.'s precuneus network (PCUN; which, in this parcellation, also includes portions of PCC and angular gyrus) because the precuneus has been implicated in episodic memory retrieval and first-person perspective taking processes (Cavanna & Trimble, 2006), which are likely to be involved in the emotion induction task.

Principal Component Analysis. Following network selection, I conducted my second data reduction step. Specifically, I used Principal Component Analysis (PCA) to reduce each network into a single representative variable (i.e., the first principal component). To conduct these analyses, I used the PCA function from the 'FactoMineR' R package (Lê, Josse, & Husson, 2008). This process reduced the ROIs within a given network to a smaller number of uncorrelated principal components representing the variability within that network. One drawback of using PCA is that some information is inevitably lost in the feature reduction process. This drawback is offset, however, by the fact that dimension reduction through PCA reduced the potential for computational burden that would have precluded me from conducting between-network connectivity analyses using GIMME. In the present analyses, the first principal component of each network served as a single variable representing a linear combination of ROIs that explained the most variability within that network. Networks with fewer ROIs tend to have higher percentages of variance explained by the first principal component, whereas networks with more ROIs tend to have lower percentages of variance explained by the first principal component. The first principal component of each network explained between 25-53% of the

variance in that network. Across conditions, the average percent of variance explained by the first principal component of each network was about 40% (M = 39.51% for the anger condition, M = 39.21% for the anxiety condition, M = 39.57% for the neutral condition, and M = 39.53% for resting state; see Table 2 for the percentage of variance explained by the first principal component of each network across conditions). Thus, the first principal component of each network accounted for a substantial amount of the variance within the given network.

Table 2. Percentage of variance explained by first principal component for each network across conditions.

Network	Number of ROIs	Anger	Anxiety	Neutral	Rest
aSAL	7	46.55	47.90	47.18	48.08
BG	5	35.94	36.98	36.55	35.79
DAN	11	25.12	27.09	27.51	27.12
dDMN	9	35.50	37.24	36.39	40.34
Lang	7	38.15	39.12	38.34	37.92
lFPC	6	44.54	40.51	47.11	43.46
PCUN	4	52.71	48.96	48.91	51.68
pSAL	12	26.20	25.53	25.35	27.09
rFPC	6	53.13	49.20	49.27	46.44
SMN	6	36.49	36.22	34.64	35.37
vDMN	10	40.35	42.58	44.07	41.51

In the present analyses, I retain only the first principal component of each network for multiple reasons. First, because my interest is in directed connectivity *between* networks, I do not wish to introduce multiple uncorrelated components from *within* networks into the model selection procedure. Second, because the S-GIMME algorithm uses a block-Toeplitz structure for model estimation, the number of variables is doubled to account for lagged relationships, which nonlinearly increases the computation time. Finally, given the number of networks I am interested in, retaining multiple principal components per network would push this application past the boundary of any existing simulation work evaluating the performance of S-GIMME. Data reduction techniques are frequently used in the network literature to get estimates of brain regions that show correlated functional activity (i.e., regions that form a network). Importantly,

simulations have demonstrated that GIMME performs similarly well in terms of true path recovery when using the first principal component derived from PCA as compared to other forms of data reduction (e.g., scaling indicators, sum scores, pseudo-ML, and model-implied instrumental variables with two-stage least square; (Gates, Fisher, & Bollen, 2020). For simplicity, I will henceforth refer to the first principal component of each network as that network (e.g., the first principal component of the dorsal attention network will be referred to as "dorsal attention network" or "DAN").

Subgrouping GIMME

I implemented the S-GIMME algorithm on the eleven networks of interest using the 'GIMME' R package (Lane, Gates, & Molenaar, 2016). I first ran S-GIMME on both conditions together to assess whether I could recover the experimental conditions participants completed (i.e., anger and anxiety) on the basis of their connectivity patterns. Next, I ran the analysis separately for the two emotion conditions to better characterize heterogeneity within an induced emotional state. Finally, I ran the S-GIMME procedure on the neutral and resting state scans to rule out the alternate hypothesis that the algorithm is simply selecting on stable individual differences that would also be present during task-positive and/or task-negative states.

During GIMME's classification procedure, a similarity matrix is formed representing the similarity of connections for each pair of individuals. This similarity matrix represents the number of connections that each pair of individuals has in common, as defined by 1) having above-threshold significance, and 2) having the same sign. During the subgrouping procedure, S-GIMME employs the Walktrap community detection algorithm (Pons & Latapy, 2005) to assign individuals to subgroups in an unsupervised manner based on the similarity of their connections to those of other individuals. Unsupervised classification does not start with a prespecified

number of subgroups into which individuals are categorized. Rather, individuals are categorized into the number of subgroups that best captures the similarities within the subgroups and the differences between them. I then probed those subgroups based on individual difference measures collected during the experiment. In this way, there are no top-down constraints on the classification of individuals into subgroups, leaving open the possibility that no subgroups are identified on the basis of participants' connectivity patterns. This procedure also avoids the pitfalls of confirmatory and seed-based approaches, which may focus exclusively on specific brain networks or regions that are thought to be important for a given cognitive task.

S-GIMME arrived at individual-, subgroup-, and group-level connectivity maps representing neural activation during the anger and anxiety runs (separately and combined), as well as during the neutral and resting state runs. The present analyses focus on subgroup-level connectivity. For all search levels, the S-GIMME algorithm revealed temporal patterns of activation across networks. These patterns included paths that were contemporaneous (i.e., activation in both networks occurred at the same point in time) as well as lagged (i.e., activation in the networks occurred at separate points in time; Beltz & Gates, 2017). It is important to note that because the temporal resolution of fMRI (seconds) is slower than the biological process it aims to capture (milliseconds), some relationships that are truly lagged may be revealed as contemporaneous (Lane et al., 2019). Thus, the present analyses give equal evaluative weight to both contemporaneous and lagged paths.

Characterizing Subgroups. I visually evaluated subgroups based on their connectivity patterns, and characterized them based on individual difference measures collected during the experiment. These measures were the VAS ratings of what participants experienced while in the scanner (i.e., the degree of anger, anxiety, activation, and unpleasantness experienced during

each run), the post-scan measures of emotional complexity (RDEES) and alexithymia (TAS-20), and participants' self-reports of what they chose to imagine to evoke emotional experiences in the scanner. Depending on the number of subgroups revealed for a given condition, I assessed differences in these measures using *t*-tests and analysis of variance, as well as their non-parametric equivalents (Mann-Whitney *U*-test and Kruskal-Wallis *H*-test, respectively). I also assessed whether there were differences between subgroups in demographic factors (e.g., age, sex, number of years of music training). To assess differences in age and years of music training, I used *t*-tests and analysis of variance, whereas to assess differences in sex, I used Chi-square tests for independence.

CHAPTER 3: ANALYSIS 1 – RECOVERING EXPERIMENTAL CONDITIONS VIA S-GIMME

My first goal was to assess whether the subgrouping procedure could reproduce the experimental conditions (i.e., anger v. anxiety) on the basis of participants' connectivity patterns. This first analysis served as a validation of the S-GIMME procedure by assessing whether S-GIMME could produce sub-groups where they should reasonably exist. I thus implemented S-GIMME on the ROI time-series-derived PCAs for each participant for each of the emotion conditions (i.e., the anxiety run and the anger run). Note that if S-GIMME were only sensitive to something like individual differences, it could have reasonably revealed subgroups corresponding to individual participants (e.g., a subgroup representing the anger and anxiety runs for participant 1, a subgroup for participant 2, a subgroup for participant 3, etc.). Rather, if S-GIMME revealed subgroups consisting of time-series representing anger v. anxiety runs irrespective of participant, then this would be evidence that it was reliably detecting brain differences that are a product of the experimental manipulation (i.e., emotion experiences). I predicted that the latter would occur.

Analysis 1: Combined Conditions

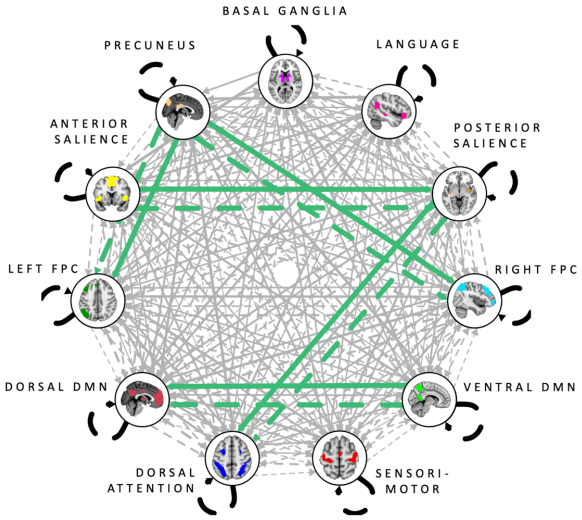
To conduct this analysis, I combined the data from the anger and anxiety conditions such that each participant contributed two time series to the sample. After implementing the S-GIMME procedure, I visually assessed differences in connectivity patterns across the subgroups revealed during the combined analysis. I then created a crosstabulation of subgroup membership and experimental condition. I assessed the degree to which the subgroups revealed corresponded

to the experimental conditions participants completed. I was specifically interested in whether brain states from the anger and anxiety conditions were classified into the same v. separate subgroups. Finally, I compared the subgroups based on VAS ratings of what participants experienced while in the scanner.

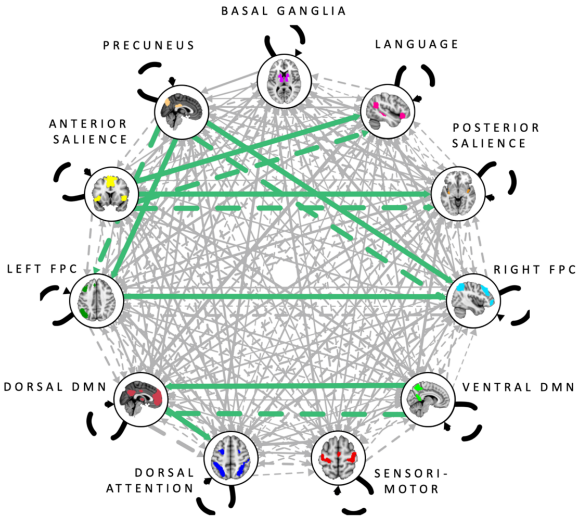
Subgroup connectivity. S-GIMME revealed three major subgroups[1] of neural responses across the experience of anger and anxiety. Subgroup 1 (n = 22)[2] had connectivity within subnetworks of SAL (from aSAL to pSAL) and DMN (from vDMN to dDMN). Subgroup 1 was also characterized by connectivity from posterior SAL to DAN, as well as from PCUN to both subnetworks of FPC. As with Subgroup 1, Subgroup 2 (n = 13) had connectivity within subnetworks of SAL (from aSAL to pSAL) and DMN (from vDMN to dDMN). Subgroup 2 also had connectivity from lFPC to rFPC, as well as connectivity from anterior SAL to Lang, both of which were not present in Subgroup 1. However, Subgroup 2 was not characterized by connectivity between posterior SAL and DAN. Finally, Subgroup 3 (n = 11) had several between-network paths that were not present in Subgroups 1 and 2. Specifically, Subgroup 3 had connectivity from dorsal DMN to PCUN, from Lang to dorsal DMN, and from BG to SMN, anterior SAL, and right FPC. Interestingly, Subgroup 3 did not have within-network connectivity between the subnetworks of DMN. Subgroups 1-3 are depicted in Figure 1.

[1] Major subgroups were defined *a priori* as consisting of data from four or more individuals. Two subgroups included anger data from only one individual per subgroup. Thus, data from those two individuals' anger runs (one per subgroup) are not characterized in the combined anger and anxiety analyses.

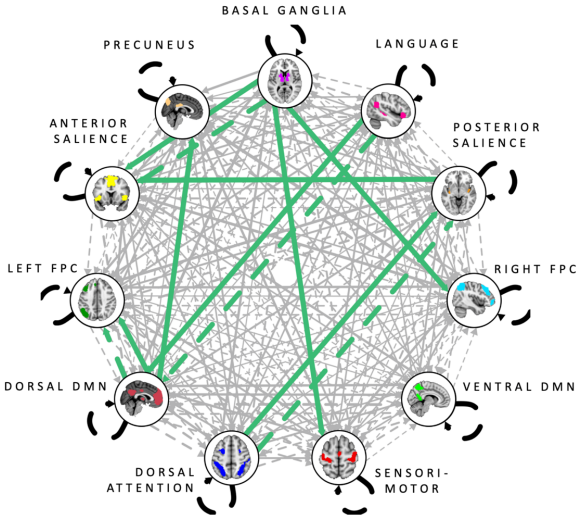
[2] For the combined analysis, each participant contributed data from two runs (the anger condition and the anxiety condition). Thus, "n" in this case refers to the number of brain states rather than the number of participants included in each subgroup.



Subgroup 1



Subgroup 2



Subgroup 3

Figure 1. Subgroup-level connectivity maps across anger and anxiety. S-GIMME revealed three subgroups of connectivity patterns during the experience of anger and anxiety. Solid lines represent contemporaneous relationships and dashed lines represent lagged (X at time-1 predicts Y at time) relationships. Autoregressive paths (X at time-1 predicts X at time) appear as dashed loops. All subgroup-level paths (green) were significant for at least 75% of the brain states within that subgroup. Individual-level paths (gray) represent each path that exists for at least one brain state within the subgroup.

I investigated whether connectivity patterns from the anger and anxiety conditions clustered meaningfully into the three subgroups. I found that Subgroup 1 was primarily composed of brain states from the anger condition (64%), whereas Subgroup 3 was primarily composed of brain states from the anxiety condition (82%). Subgroup 2 was approximately evenly split, containing similar numbers of brain states from both the anger (46%) and anxiety (54%) conditions (see Figure 2). The connectivity maps for Subgroups 1 and 3 lend themselves to interpretation in terms of the emotion that is predominantly represented in each subgroup. For Subgroup 1 (the *de facto* Anger Subgroup), greater SAL to DAN connectivity suggests that SAL is directing DAN to salient events so that participants can engage in goal-directed stimulus and response selection (Corbetta & Schulman, 2002). This finding is also consistent with work showing greater intensity of activation in DAN during the experience of anger as compared to other categories of emotion (Wager et al., 2015). In addition, Wager et al., (2015) found greater intensity of activation in FPC and DMN during the experience of anger as compared to fear, mapping onto Subgroup 1, which is characterized by connectivity between FPC and PCUN (a major node of DMN; Utevsky, Smith, & Huettel, 2014). For Subgroup 3 (the *de facto* Anxiety Subgroup), the presence of directed connectivity from BG to aSAL and rFPC is consistent with seed-based analyses demonstrating that increased connectivity between nuclei of the basal ganglia and regions of FPC and aSAL are associated with social anxiety disorder (Anteraper et al., 2014). Further, Subgroup 3's lack of within-network DMN connectivity is consistent with recent work showing that anxiety is associated with reduced functional connectivity in regions of the DMN (Imperatori et al., 2019; Modi, Kumar, Kumar, & Khushu, 2015). Finally, finding that Subgroup 3 had greater connectivity between BG and SMN is consistent with Wager et al., 2015,

who found greater intensity of activation between these networks during the experience of fear as compared to anger.

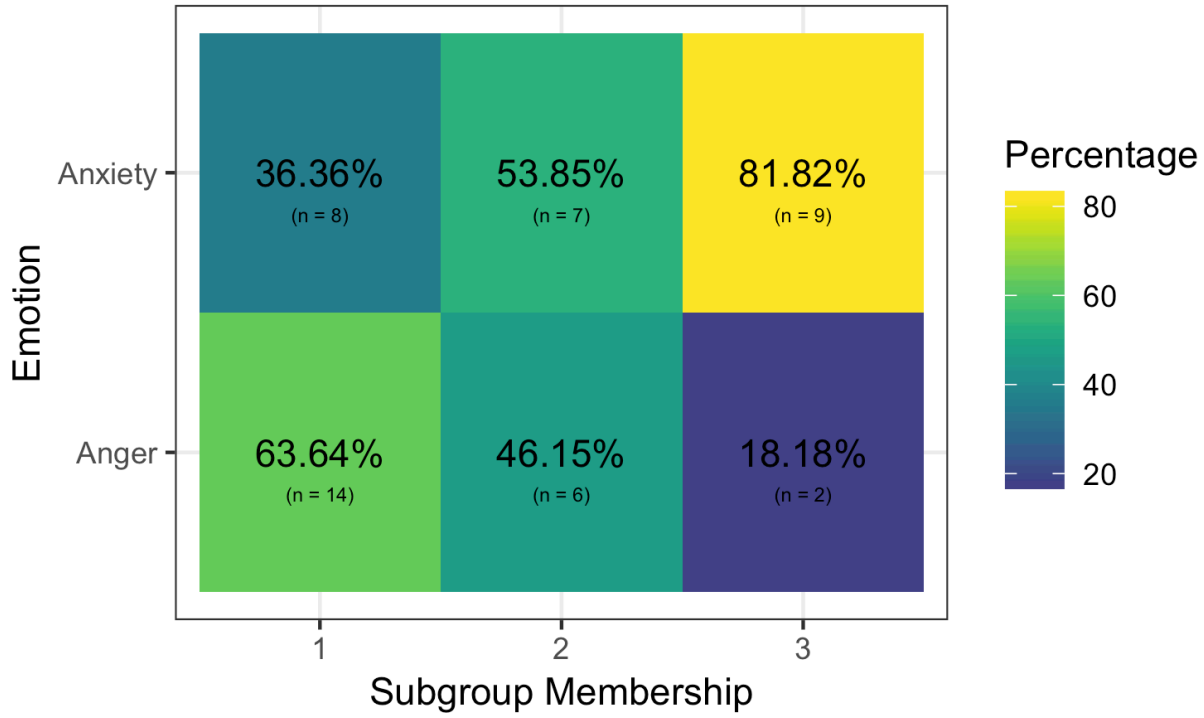


Figure 2. Percentages of anger and anxiety brain states in each subgroup. Subgroup 1 was composed of 64% anger brain states and 36% anxiety brain states, whereas Subgroup 3 was composed of 82% anxiety brain states and 18% anger brain states. Subgroup 2 contained an approximately even split of anger and anxiety brain states.

Post-scan measures. The subgrouping procedure generally recovered the experimental conditions to which participants were assigned (i.e., Subgroup 1 predominantly consisted of brain states from the anger run, and Subgroup 3 predominantly consisted of brain states from the anxiety run). I used Student's *t*-tests to examine whether participants' self-reported VAS ratings of anger and anxiety conformed to these subgroups. Note that because each participant contributed two brain states to the combined analysis (one from the anger induction and one from the anxiety induction), comparisons between subgroups are not fully independent.

However, separate VAS scores were collected following both emotion inductions. Thus, the following analyses will treat individual VAS scores as the unit of measurement.

I failed to observe differences in self-reported emotion when comparing each of the three subgroups of brain states on corresponding participants' reported levels of anger or anxiety (ps > .10). This likely reflects the fact that each subgroup contained some proportion of brain states from participants in both conditions. However, participants in the anxiety condition who were classified into the *de facto* anxiety subgroup on the basis of their brain processes rated significantly more anxiety (M = 4.44) than participants in the anger condition who were classified into the *de facto* anxiety subgroup (M = 2.30), $t(5.80) = -3.15$, $p = .02$, $d = 1.36$. In contrast, participants in the anger condition who were classified into the *de facto* anxiety subgroup on the basis of their brain processes did not differ in their reports of anger as compared to participants in the anxiety condition ($p > .1$).

Similarly, participants in the anger condition who were classified into the *de facto* anger subgroup on the basis of their brain processes rated significantly more anger (M = 4.90) than participants in the anxiety condition who were classified into the *de facto* anger subgroup (M = 1.79), $t(19.64) = 4.50$, $p < .001$, $d = 1.77$. Participants in the anxiety condition who were classified into the *de facto* anger subgroup on the basis of their brain processes reported marginally more anxiety (M = 5.46) than participants in the anger condition (M = 3.40), $t(14.59) = -1.84$, $p = .09$, $d = .82$.

Finally, participants in the anger and anxiety conditions who were classified into the mixed subgroup (i.e., Subgroup 2) did not differ significantly in their reports of anger or anxiety based on assigned condition (ps > .1).

In summary, analysis 1 revealed that the subgrouping procedure was able to roughly reproduce the experimental conditions (i.e., anger v. anxiety) on the basis of participants' connectivity patterns. Importantly, the procedure did not reveal subgroups corresponding to each participant, which plausibly could have occurred if S-GIMME was insensitive to the evoked emotional state. This finding suggests that the S-GIMME procedure is detecting true variation in connectivity related to each experimental condition, thus serving as a validation of the present task and analysis approach.

CHAPTER 4: ANALYSIS 2 – IDENTIFYING NEURAL DEGENERACY WITHIN ANGER AND ANXIETY

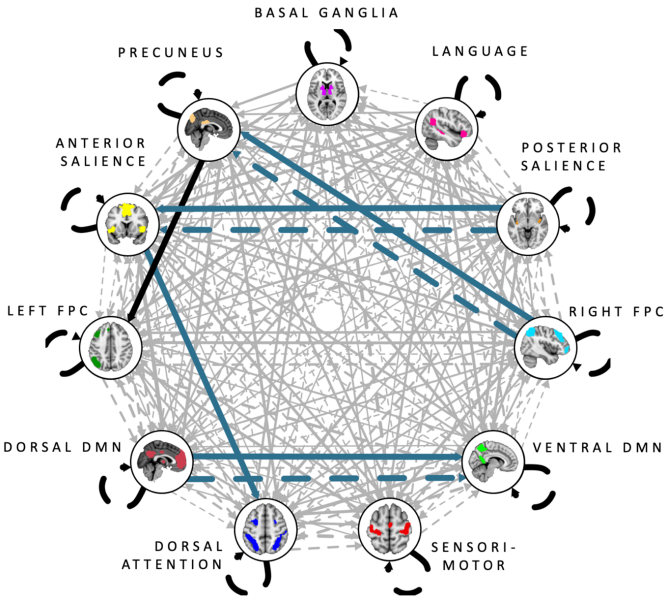
The findings from analysis 1 provide a proof-of-concept that the S-GIMME algorithm is picking up on true variation related to the experimental conditions, but the most important question is whether this variation can be further sub-divided into distinct patterns of connectivity within each emotion category. Finding subgroups with distinct patterns of connectivity during the same emotional experience would provide the first evidence for degeneracy in the brain basis of emotion. For analysis 2, I implemented S-GIMME on the data from each of the emotion runs separately (i.e., the anger run and the anxiety run) to examine whether degenerate functional connectivity patterns existed within those conditions. Within each run, I compared subgroups revealed by S-GIMME based on the presence of paths between networks, and characterized those subgroups based on differences in VAS ratings. I was particularly interested in whether there were differences between subgroups in the extent to which they experienced anger or anxiety during the corresponding scans. For example, if the S-GIMME procedure reveals subgroups that do not differ in their VAS ratings of anger during the anger condition, it would provide evidence for degenerate neural representations of anger. Following my analysis of VAS ratings, I assessed differences between subgroups in the post-scan measures of emotion (i.e., RDEES and TAS-20) and participants' self-reports of what they chose to imagine to evoke an emotional experience while in the scanner. Finally, I assessed the cross-categorization of participants within the subgroups revealed during the anger and anxiety conditions.

Analysis 2a: Anger Condition

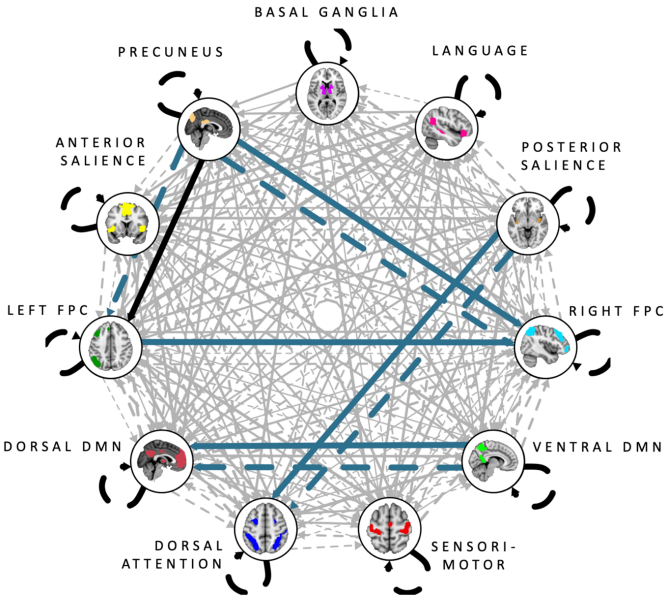
To conduct this analysis, I implemented the S-GIMME procedure on the time series from the anger condition. For any subgroups revealed, I visually assessed differences in the presence v. absence of paths between networks during the anger condition. Next, I compared the subgroups based on VAS ratings of what participants experienced while in the scanner, with a particular focus on whether the subgroups experienced the same v. different degrees of anger during the task. Finally, I compared the subgroups based on individual difference measures of emotional complexity (RDEES) and alexithymia (TAS-20), as well as any potential differences in what participants chose to imagine while in the scanner.

Subgroup connectivity. S-GIMME revealed two major subgroups of individuals[3] based on their patterns of connectivity during the anger condition. Subgroup 1 (N = 10) had connectivity between subnetworks of SAL (from pSAL to aSAL) and DMN (from dDMN to vDMN), as well as connectivity from aSAL to DAN. Subgroup 2 (N = 12) also had connectivity between subnetworks of DMN (from vDMN to dDMN), but uniquely had connectivity between subnetworks of FPC (from lFPC to rFPC), and no connectivity between subnetworks of SAL. Subgroup 2 was also characterized by additional connectivity from pSAL to DAN. In addition to the subgroup-level paths, there was a group-level path between PCUN and lFPC, meaning that this path was present for at least 75% of individuals during the experience of anger. Notably, this path was also present at the subgroup-level in the de facto anger subgroup revealed in analysis 1. Subgroup-level connectivity maps for Subgroups 1 and 2 are depicted in Figure 3.

[3] As previously noted, major subgroups were defined *a priori* as consisting of data from four or more individuals. Two individuals comprised a third "subgroup" which was not characterized because it did not meet this criterion.



Subgroup 1



Subgroup 2

Figure 3. Subgroup-level connectivity maps for anger. S-GIMME revealed two subgroups of connectivity patterns during the experience of anger. Solid lines represent contemporaneous relationships and dashed lines represent lagged (X at time-1 predicts Y at time) relationships. Autoregressive paths (X at time-1 predicts X at time) appear as dashed loops. One contemporaneous group-level path (black) from PCUN to lFPC was significant for at least 75% of individuals across both subgroups. All subgroup-level paths (blue) were significant for at least 75% of individuals within each subgroup. Individual-level paths (gray) represent each path that exists for at least one individual within the subgroup.

Music training and demographic measures. Because prior work has shown that musicians process music differently than those with no music training (Angulo-Perkins et al., 2014; Ohnishi et al., 2001; Seung, Kyong, Woo, Lee, & Lee, 2005), I first investigated whether the two subgroups revealed by S-GIMME differed in number of years of self-taught or formal music training. A Student's *t*-test revealed that Subgroup 1 (M = 3.80) and Subgroup 2 (M = 4.50) did not differ in number of years of music training (p =.80). I also investigated whether the two subgroups differed on key demographic variables. Specifically, I compared average age across the two subgroups, and I assessed whether the classification into subgroups depended on sex. A Student's *t*-test revealed that Subgroup 1 (M = 21.20) and Subgroup 2 (M = 24.33) did not significantly differ in age (p =.14), and a Pearson's Chi-square test for independence with Yates' continuity correction revealed that subgroup classification was independent of sex, $\chi^2\ (1, N = 24) = 0.002,\ p = 0.97$. I next assessed whether there were any significant differences in the post-scan measures of emotion.

Post-scan measures. I used Student's *t*-tests to assess mean differences between subgroups in the measures of emotion that were collected after each run (i.e., VAS ratings of the intensity of anger, anxiety, unpleasantness, and activation), as well as the RDEES and TAS-20 questionnaire responses. Critically, consistent with my hypothesis that different patterns of neural activation can produce the same emotion, there was no difference between Subgroup 1 (M = 5.08) and Subgroup 2 (M = 3.65) in the intensity of anger experienced (p =.11). However, differences in neural representations during the experience of anger may have been related to differences in the features that each subgroup experienced as part of anger. For instance, Subgroup 1 experienced anger as significantly more unpleasant (M = 4.91) as compared to

Subgroup 2 (M = 2.81), t(15.45) = 2.72, p = .02, Cohen's d = 1.21, 95% CI [0.24, 2.18]. This finding suggests that greater within-network connectivity in SAL in Subgroup 1 may confer relatively more unpleasant anger experiences. Prior meta-analytic work has linked activation within regions that comprise SAL with the experience of unpleasant affect (Lindquist, Satpute, Wager, Weber, & Barrett, 2016) and fluctuations within SAL are associated with greater self-reported intensity of negative affect (Seeley et al., 2007; Touroutoglou, Hollenbeck, Dickerson, & Barrett, 2012).

In addition to observing differences in the features of participants' experienced anger, I also found that Subgroup 1 contained participants who scored, on average, higher on the Toronto Alexithymia Scale (M = 44.20) as compared to Subgroup 2 (M = 37.67), t(18.99) = 2.51, p = .02, Cohen's d = 1.04, 95% CI [0.08, 1.99]. Alexithymia is a construct characterized by difficulty describing one's feelings and is associated with experiencing greater intensity of negative affect and physiological activation (Byrne & Ditto, 2005; Friedlander, Lumley, Farchione, & Doyal, 1997; Luminet, Rimé, Bagby, & Taylor, 2004). Subgroups did not differ in emotional complexity as measured by scores on the RDEES, they did not differ in VAS ratings of anxiety and activation, and they did not differ in their self-reports of what they imagined while generating experiences of anger in the scanner (ps > .10). See Table 3 for results from all tests, as well as their nonparametric equivalents.

Table 3. Parametric (Student's *t*-test) and Nonparametric (Mann-Whitney *U*-test) Comparisons of Anger Subgroups 1 and 2

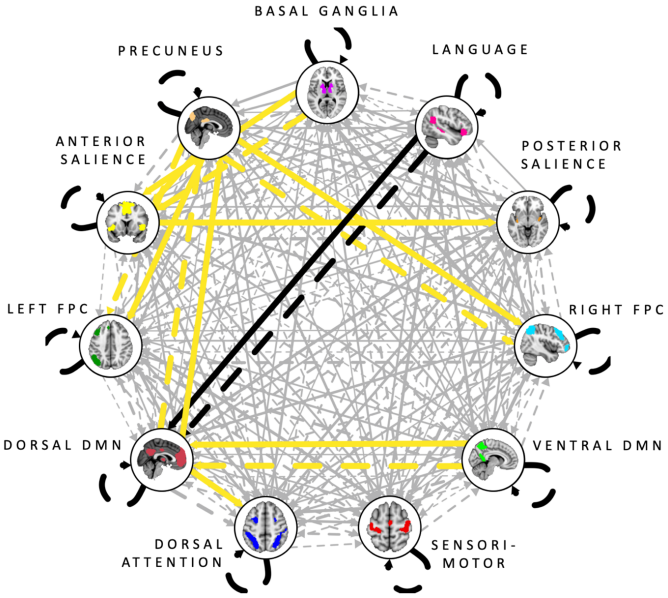
Measure	Subscale	Parametric Test	Nonparametric Test
VAS	Anger	$t = 1.66$, $p = 0.11$	$U = 81.5$, $p = 0.17$
	Anxiety	$t = 1.04$, $p = 0.31$	$U = 74.5$, $p = 0.36$
	Activation	$t = -0.68$, $p = 0.51$	$U = 48.5$, $p = 0.47$
	Unpleasantness	$t = 2.72$, $p = 0.02$	$U = 96.5$, $p = 0.02$
TAS-20	Overall Score	$t = 2.51$, $p = 0.02$	$U = 90$, $p = 0.05$
	Difficulty Describing Feelings	$t = 3.10$, $p = 0.01$	$U = 101.5$, $p = 0.01$
	Difficulty Identifying Feelings	$t = 1.87$, $p = 0.08$	$U = 85.5$, $p = 0.10$
	Externally-Oriented Thinking	$t = -0.98$, $p = 0.34$	$U = 42$, $p = 0.24$
RDEES	Overall Score	$t = 0.20$, $p = 0.85$	$U = 60$, $p = 1.00$
	Range	$t = 0.75$, $p = 0.46$	$U = 70$, $p = 0.53$
	Differentiation	$t = -0.50$, $p = 0.62$	$U = 53$, $p = 0.67$
Self-reported descriptions of what participants chose to think about while in the scanner	Frequency of Emotion Words Used	$t = 1.23$, $p = 0.25$	$U = 54$, $p = 0.27$
	Frequency of Valence Words Used	$t = 0.88$, $p = 0.40$	$U = 50$, $p = 0.48$
	Frequency of Arousal Words Used	$t = -0.80$, $p = 0.44$	$U = 35.5$, $p = 0.55$
	Frequency of Body Words Used	$t = 1.00$, $p = 0.36$	$U = 48$, $p = 0.23$
	Internal v. External Scenario	$t = 0.56$, $p = 0.59$	$U = 43$, $p = 0.96$
	Social vs. Nonsocial Scenario	$t = 1.49$, $p = 0.17$	$U = 39$, $p = 0.18$
	Remembered v. Imagined Scenario	$t = 0.83$, $p = 0.42$	$U = 45$, $p = 0.51$

Although participants had the same experience of anger during the anger induction, the features and corresponding neural representations of their experiences differed across subgroups. These findings demonstrate initial evidence for degeneracy across participants in the experience of anger. Following my analysis of subgroup differences during the experience of anger, I investigated differences in subgroups revealed during the experience of anxiety.

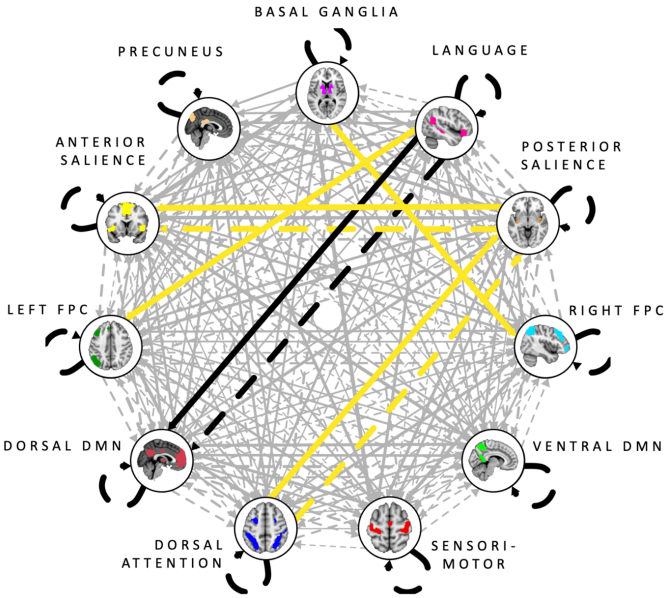
Analysis 2b: Anxiety Condition

To conduct this analysis, I implemented the S-GIMME procedure on the time series from the anxiety condition. For any subgroups revealed, I visually assessed differences in the presence v. absence of paths between networks during the anxiety condition. Next, I compared the subgroups based on VAS ratings of what participants experienced while in the scanner, with a particular focus on whether the subgroups experienced the same v. differing degrees of anxiety during the task. Finally, I compared the subgroups based on individual difference measures of emotional complexity (RDEES) and alexithymia (TAS-20), as well as any potential differences in what participants chose to imagine to evoke an experience of anxiety while in the scanner.

Subgroup connectivity. An analysis of the anxiety condition revealed two subgroups of individuals based on their connectivity patterns. Subgroup 1 (N = 12) had greater connectivity between subnetworks of SAL (from aSAL to pSAL) and DMN (from vDMN to dDMN). Individuals in Subgroup 1 also had connectivity from PCUN to both subnetworks of FPC, as well as from PCUN to aSAL (none of which surfaced consistently in Subgroup 2). Finally, Subgroup 1 had connectivity from dDMN to PCUN and from dDMN to DAN. Subgroup 2 (N = 12) had connectivity between the subnetworks of SAL (from pSAL to aSAL), but not between subnetworks of DMN, and was characterized by connectivity from DAN to pSAL. Subgroup 2 also had connectivity from Lang to lFPC, as well as from BG to rFPC. There was also a group-level path between Lang and dDMN, meaning that this path was present for at least 75% of individuals across both subgroups during the experience of anxiety. Interestingly, this path also emerged as a subgroup-level path in the *de facto* anxiety subgroup revealed in analysis 1. Subgroup-level connectivity maps for Subgroups 1 and 2 are depicted in Figure 4.



Subgroup 1



Subgroup 2

Figure 4. Subgroup-level connectivity maps for anxiety. S-GIMME revealed two subgroups of connectivity patterns during the experience of anxiety. Solid lines represent contemporaneous relationships and dashed lines represent lagged (X at time-1 predicts Y at time) relationships. Autoregressive paths (X at time-1 predicts X at time) appear as dashed loops. Contemporaneous and lagged group-level paths (black) from Lang to dDMN were significant for at least 75% of individuals across subgroups. All subgroup-level paths (yellow) were significant for at least 75% of individuals within each subgroup. Individual-level paths (gray) represent each path that exists for at least one individual within the subgroup.

Music training and demographic measures. As with the anger induction, a Student's *t*-test revealed that Subgroup 1 (M = 4.17) and Subgroup 2 (M = 3.92) did not differ in number of years of music training (p = .92). Similarly, a Student's *t*-test revealed that Subgroup 1 (M = 23.33) and Subgroup 2 (M = 22.50) did not significantly differ in age (p = .69), and a Pearson's Chi-square test for independence with Yates' continuity correction revealed that subgroup classification was independent of sex, $\chi^2\ (1, N = 24) = 0.000,\ p = 1.00$. I next assessed whether there were any significant differences between subgroups in the post-scan measures collected.

Post-scan measures. I again used Student's *t*-tests to assess differences between the subgroups identified by the S-GIMME procedure. Subgroup 2 experienced greater intensity of self-reported anxiety (M = 5.66) as compared to Subgroup 1 (M = 3.99), $t(21.31)$ = -2.26, p = .03, Cohen's d = -.92, 95% CI [-1.81, 0.03]. However, this effect was not present in the non-parametric analysis (p = 0.16), and it appeared to be largely driven by a potential outlier in the parametric analysis.[4] I calculated Cook's Distance to assess whether this potential outlier had undue leverage on the results. Using the recommended threshold of $D_i > \frac{4}{n-k-1}$ where n is the sample size and k is the number of independent variables in the model (Chatterjee & Hadi, 1988), I determined that the suspected outlier was indeed having undue leverage. More specifically, the threshold for undue leverage is $\frac{4}{24-1-1} = .18$ and the outlying data point has a Cook's Distance value of .29. I conducted a sensitivity analysis by removing the outlier and recomputing the parametric test. Without this outlier, the difference in self-reported anxiety between Subgroup 1 (M = 3.99) and Subgroup 2 (M = 5.26) is only marginal (p =.06).

[4] The outlying individual reported on a scale of 1-10 that their anxiety level was 10, but their unpleasantness level was 2.4 and their activation level was 3.6 (raw scores). This case was not a data entry mistake, but I cannot rule out whether it was recorded incorrectly during the scan or whether the participant mislabeled his/her state.

As with the anger condition, subgroups revealed during the anxiety condition differed in the features that they experienced as part of their experience of anxiety. Subgroup 1 tended to contain participants who scored higher on the Difficulty Identifying Feeling (DIF) Subscale of the Toronto Alexithymia Scale (M = 15.33) as compared to Subgroup 2 (M = 12.00), $t(21.47)$ = 2.30, p = .03, Cohen's d = .94, 95% CI [0.05, 1.83]. The finding that Subgroup 1 scored higher on the DIF subscale and had less connectivity between Lang and lFPC may reflect difficulty in the semantic selection and retrieval necessary to reflect upon and label one's emotional state (Chiou, Humphreys, Jung, & Lambon Ralph, 2018; Hirshorn & Thompson-Schill, 2006; Klein, Milner, Zatorre, Meyer, & Evans, 2006; Whitney, Kirk, O'Sullivan, Lambon Ralph, & Jefferies, 2011). Subgroups revealed during the anxiety condition did not differ in emotional complexity as measured by scores on the RDEES, nor did they differ in their VAS ratings of unpleasantness, activation, and anger experienced during the anxiety induction (ps > .10). There was, however, a marginal difference in participants' self-reports such that Subgroup 2 focused marginally more on imagined v. prospective scenarios while generating experiences of anxiety in the scanner (p = .08). See Table 4 for results from all tests, as well as their nonparametric equivalents.

Table 4. Parametric (Student's *t*-test) and Nonparametric (Mann-Whitney *U*-test) Comparisons of Anxiety Subgroups 1 and 2

Measure	Subscale	Parametric Test	Nonparametric Test
VAS	Anger	$t = 0.67$, $p = 0.51$	$U = 74.5$, $p = 0.91$
	Anxiety	$t = -2.26$, $p = 0.03$	$U = 42.5$, $p = 0.16$
	Activation	$t = -0.41$, $p = 0.68$	$U = 61.5$, $p = 0.56$
	Unpleasantness	$t = -0.85$, $p = 0.41$	$U = 62.5$, $p = 0.60$
TAS-20	Overall Score	$t = 1.27$, $p = 0.22$	$U = 95$, $p = 0.19$
	Difficulty Describing Feelings	$t = 1.00$, $p = 0.33$	$U = 87.5$, $p = 0.38$
	Difficulty Identifying Feelings	$t = 2.30$, $p = 0.03$	$U = 107$, $p = 0.05$
	Externally-Oriented Thinking	$t = -1.21$, $p = 0.24$	$U = 50$, $p = 0.21$
RDEES	Overall Score	$t = 0.66$, $p = 0.52$	$U = 80.5$, $p = 0.64$
	Range	$t = 0.64$, $p = 0.53$	$U = 80.5$, $p = 0.64$
	Differentiation	$t = 0.42$, $p = 0.68$	$U = 81.5$, $p = 0.60$
Self-reported descriptions of what participants chose to think about while in the scanner	Frequency of Emotion Words Used	$t = 0.00$, $p = 1.00$	$U = 52$, $p = 0.90$
	Frequency of Valence Words Used	$t = 0.00$, $p = 1.00$	$U = 51$, $p = 0.96$
	Frequency of Arousal Words Used	$t = 0.37$, $p = 0.71$	$U = 58$, $p = 0.48$
	Frequency of Body Words Used	$t = 0.00$, $p = 1.00$	$U = 50$, $p = 1.00$
	Internal v. External Scenario	$t = 0.26$, $p = 0.80$	$U = 47$, $p = 0.84$
	Social vs. Nonsocial Scenario	$t = 0.52$, $p = 0.61$	$U = 52$, $p = 0.87$
	Remembered v. Imagined Scenario	$t = -1.87$, $p = 0.08$	$U = 23.5$, $p = 0.10$

Analysis of the anxiety condition revealed that participants in both subgroups had similar experiences of anxiety (with the caveat that one outlier was removed because that individual was having undue leverage on the results). Additionally, as in the anger condition, the features and corresponding neural representations of participants' experiences differed across subgroups. Taken together, the findings from the anger and anxiety conditions provide further evidence for degeneracy across participants in the brain basis of emotion experience.

Analysis 2c: Subgroup Membership Across Runs

Following my analysis of the subgroups revealed during the anger and anxiety conditions, I investigated whether the same individuals tended to cluster together across the two conditions. If individuals clustered together, it would suggest that some stable person-level factor caused them to have similar brain patterns across distinct emotions (e.g., some people may rely more on autobiographical memories when experiencing emotions than others, which may result in a subgroup characterized by greater connectivity between PCUN and subnetworks of DMN). Alternatively, if individuals are not more likely to share the same subgroup across conditions, it would suggest even greater stochasticity in the degenerate neural response to emotion than previously uncovered.

To conduct this analysis, I created an alluvial diagram using the alluvial function from the 'alluvial' R package (Bojanowski & Edwards, 2016). The alluvial function takes as input a dataset indicating the subgroup to which participants were assigned for each condition. The dataset included one column corresponding to each condition (i.e., anger and anxiety) and one column of frequencies. The condition column contained the subgroup that a participant might be classified into (e.g., Subgroup 1), and the frequency column contained the number of participants that shared the same pattern of subgroup membership across the two conditions (i.e., the number of participants that were assigned to Subgroup 1 for anger and Subgroup 1 for anxiety, the number of participants that were assigned to Subgroup 1 for anger and Subgroup 2 for anxiety, and so on). The alluvial function produces a visualization of the cross-categorization of participants into anger and anxiety subgroups (Figure 5).

Consistent with my predictions, individuals did not tend to cluster into the same subgroups across conditions. For instance, if two participants shared the same subgroup for the

anger condition, there was a 50/50 chance that they shared the same subgroup for the anxiety condition. Of the 10 participants in Anger Subgroup 1, five were in Anxiety Subgroup 1 and five were in Anxiety Subgroup 2. Of the 12 participants in Anger Subgroup 2, six were in Anxiety Subgroup 1 and six were in Anxiety Subgroup 2. Finally, of the two participants in Anger Subgroup 3 (which was not characterized above because N < 4), one was in Anxiety Subgroup 1 and one was in Anxiety Subgroup 2.

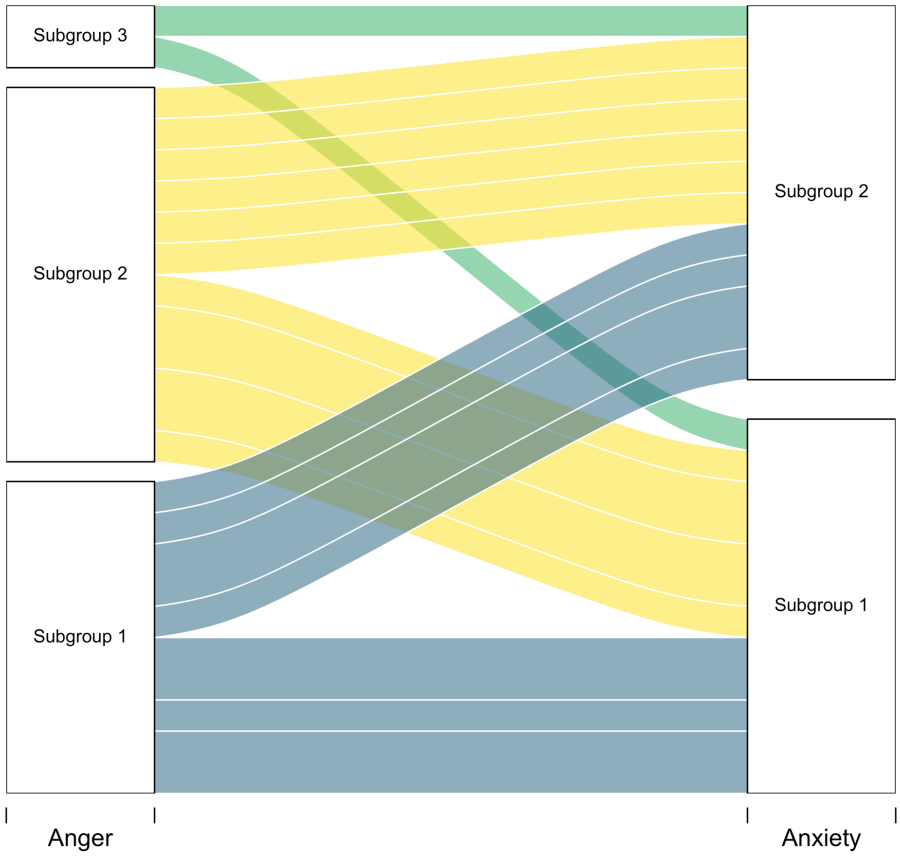


Figure 5. Subgroup membership across anger and anxiety conditions. Participants were equally likely to share the same subgroup across conditions as they were to be in different subgroups across conditions (e.g., 50% of participants in Anger Subgroup 1 were in Anxiety Subgroup 1, and the other 50% of participants in Anger Subgroup 1 were in Anxiety Subgroup 2).

Analysis 2d: Neural Representation of Emotional Complexity

As a final analysis of the anger and anxiety conditions, I investigated whether emotional complexity might be represented in the brain as within-person differences in connectivity patterns across anger and anxiety. To conduct this analysis, I quantified the number of unique paths a given participant had in their individual-level connectivity maps for anger and anxiety (i.e., paths that are not common across both anger and anxiety). I then computed a complexity ratio where the numerator is the number of unique paths, and the denominator is the total number of paths across both anger and anxiety:

$$Complexity = \frac{Unique\ Paths}{Unique + Common\ Paths}$$

Finally, I assessed whether this complexity ratio was correlated with the post-scan measure of emotional complexity (i.e., RDEES) collected in the present experiment.

I found that participants' scores on the RDEES were not significantly correlated with the complexity of their brain states as measured by the difference in connectivity patterns across anger and anxiety (p >.10). However, visual inspection of a scatterplot of these variables revealed a clear outlier who had a low score on the RDEES and a rather high ratio of brain state complexity. I conducted a sensitivity analysis by removing this outlier and re-running the test to assess whether there was any impact on the results. Without this outlier, there is a marginally significant positive correlation between scores on the RDEES and the complexity of participants' brain states across anger and anxiety, $r(22) = .39, p$ =.06). See Figure 6 for scatterplots depicting this relationship with and without the outlier (left panel and right panel, respectively). This finding provides evidence that the individual-level brain states identified by the GIMME algorithm map on to a self-report measure of the emotion. Specifically, the extent to which

participants' brain states were differentiated across anger and anxiety was marginally significantly related to participants' self-reported ability to differentiate between different emotional states.

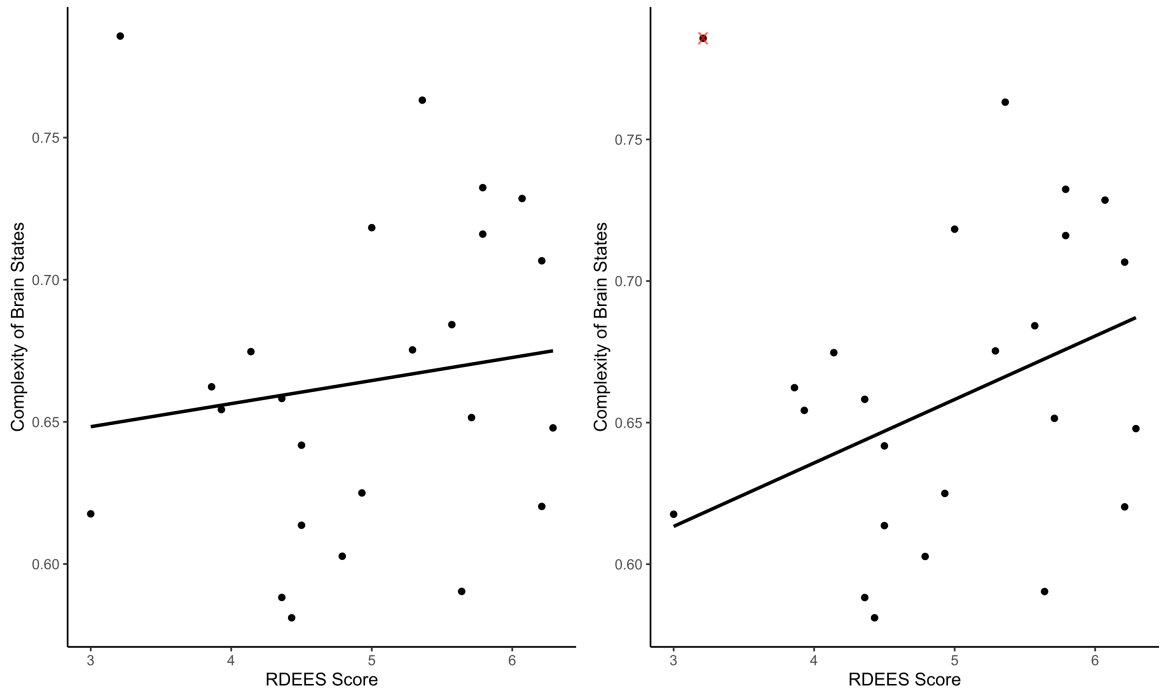


Figure 6. Relationship between complexity of brain states and scores on a self-report measure of emotional complexity. The panel on the left shows the relationship between complexity of participants' brain states (i.e., the extent to which anger and anxiety are differentiated at the neural level) and scores on the RDEES measure of emotional complexity. Although the relationship is non-significant, there appears to be a potential outlier. The panel on the right depicts the relationship between complexity of participants' brain states and scores on the RDEES after removing the outlier. This sensitivity analysis revealed a marginally significant relationship between neural and self-report measures of emotional complexity.

CHAPTER 5: ANALYSIS 3 – USING A TASK-POSITIVE CONTROL CONDITION TO RULE OUT THE POSSIBILITY THAT SUBGROUPS WERE DETERMINED BY INDIVIDUAL-LEVEL FACTORS

The above analyses of the anger and anxiety conditions suggest that degenerate neural representations are associated with the experience of emotion. Specifically, S-GIMME roughly reproduced the experimental conditions in the present task, and identified subgroups of individuals with different patterns of brain activation in response to the same emotional experience. Because individuals did not cluster together into the same subgroups across the anger and anxiety conditions, it seems unlikely that these results reflect person-level factors that are stable across distinct experiences. Nonetheless, the design of the fMRI experiment affords additional analyses that will help rule out the alternate hypothesis that the observed subgroups reflect person-level factors and are not a product of the evoked anger and anxiety states. I implemented the S-GIMME procedure on the neutral music condition in order to rule out the possibility that features of the subgroups revealed during the anger and anxiety conditions would also be present during an affectively neutral condition.

The neutral condition provides a task-positive control because participants listened to music without generating an emotional experience. I predicted that the S-GIMME algorithm would reveal subgroups of individuals during the neutral condition. I also predicted that individuals in these subgroups would likely differ in their affective responses to the neutral composition they heard during the task. These individual differences may be evident in VAS scores, self-reports of experiences during the scan, or the number of years of music training they may have received. However, I anticipated that any subgroups revealed during the neutral music

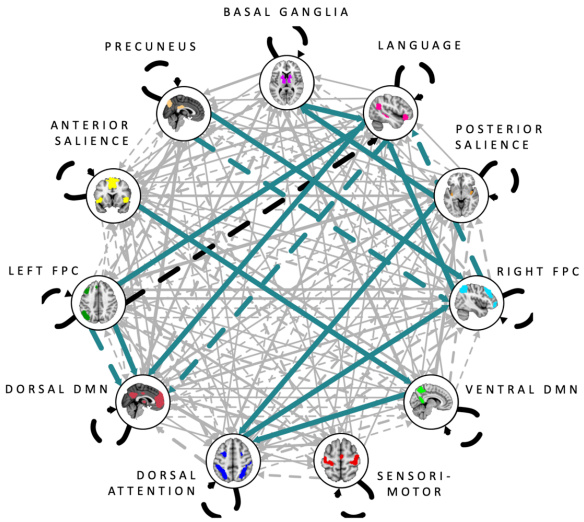
condition would not differ on individual difference measures of emotion (e.g., RDEES and TAS-20). Most importantly, I predicted that these subgroups would be different from those revealed during the anger and anxiety conditions, which would suggest that the findings from my previous analyses are a result of the evoked states rather than stable individual differences not measured in the present experiment. Confirmation of my hypotheses will provide further evidence in support of degeneracy in the brain basis of emotional experience.

Analysis 3: Neutral Condition

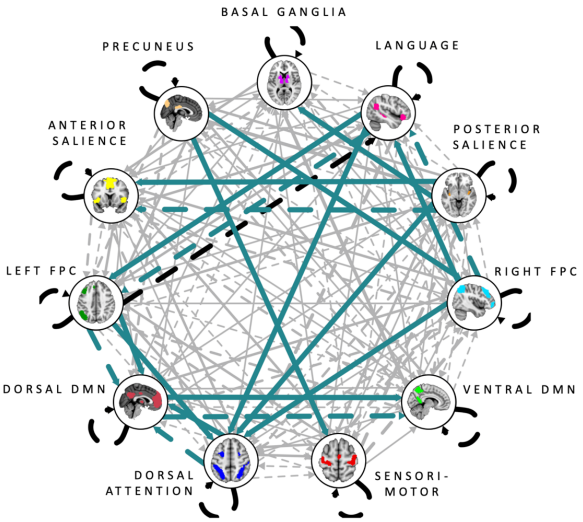
To conduct this analysis, I implemented the S-GIMME procedure on the time series from the neutral condition. For any subgroups revealed, I visually assessed differences in the presence v. absence of paths between networks during the neutral condition. I then compared the subgroups based on VAS ratings of what participants experienced while in the scanner, individual difference measures of emotional complexity (RDEES) and alexithymia (TAS-20), as well as any potential differences in what participants chose to imagine while in the scanner. Finally, I assessed the extent to which the subgroups revealed during the neutral condition differed from those revealed during the anger and anxiety conditions.

Subgroup connectivity. S-GIMME revealed four subgroups of individuals based on their brain connectivity during the neutral condition. Subgroup 1 (N = 5) was marked by less overall connectivity between subnetworks of DMN (no subgroup-level paths between dDMN, vDMN, and PCUN) and between subnetworks of FPC (no subgroup-level paths between lFPC and rFPC). Subgroup 2 (N = 5) had connectivity between subnetworks of DMN (from dDMN to vDMN), but not between subnetworks of FPC. Subgroup 3 (N = 7) had connectivity between subnetworks of DMN (from vDMN to dDMN), connectivity between subnetworks of FPC (from rFPC to lFPC), and connectivity between subnetworks of SAL (from aSAL to pSAL). Subgroup

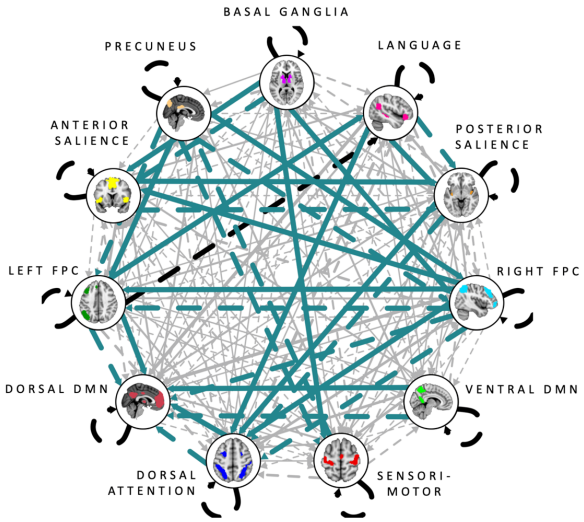
4 (N = 7) had connectivity between subnetworks of DMN (from vDMN to dDMN), and connectivity between subnetworks of SAL (from pSAL to aSAL). In addition, Subgroup 4 had connectivity from aSAL to dDMN and from vDMN to pSAL. Subgroup-level connectivity maps for Subgroups 1-4 are depicted in Figure 7.



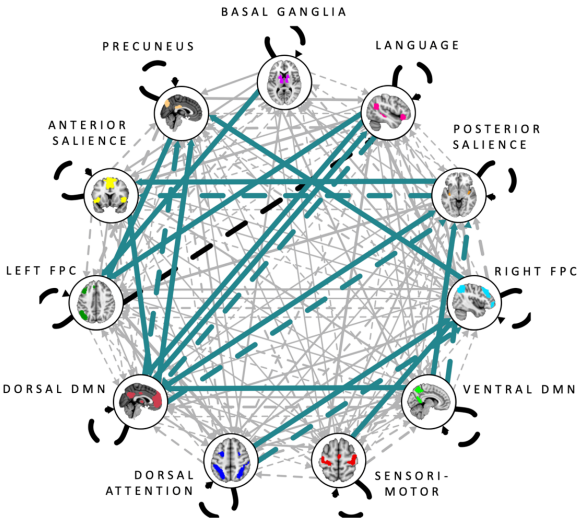
Subgroup 1



Subgroup 2



Subgroup 3



Subgroup 4

Figure 7. Subgroup-level connectivity maps for the neutral condition. S-GIMME revealed four subgroups of connectivity patterns during the neutral condition. Solid lines represent contemporaneous relationships and dashed lines represent lagged (X at time-1 predicts Y at time) relationships. Autoregressive paths (X at time-1 predicts X at time) appear as dashed loops. A lagged group-level path (black) from lFPC to Lang was significant for at least 75% of individuals across subgroups. All subgroup-level paths (teal) were significant for at least 75% of individuals within each subgroup. Individual-level paths (gray) represent each path that exists for at least one individual within the subgroup.

Music training and demographic measures. As with the anger and anxiety conditions, I assessed whether subgroups differed in terms of age, sex, or years of music training. A one-way analysis of variance revealed that Subgroup 1 (M = 5.40), Subgroup 2 (M = 6.20), Subgroup 3 (M = 1.00), and Subgroup 4 (M = 4.57) did not significantly differ in number of years of music training (p = .47). Similarly, a one-way analysis of variance revealed that Subgroup 1 (M = 23.40), Subgroup 2 (M = 20.80), Subgroup 3 (M = 22.14), and Subgroup 4 (M = 24.86) did not significantly differ in age (p = .55). Finally, a Pearson's Chi-square test for independence with Yates' continuity correction revealed that subgroup classification was independent of sex, $\chi^2\ (3, N = 24) = 4.44,\ p = 0.22$. I next assessed whether there were any significant differences in the post-scan measures of interest.

Post-scan measures. I first used analysis of variance to assess differences in VAS scores between the four subgroups identified by the S-GIMME procedure during the neutral condition. These tests revealed no differences in the extent to which participants experienced feelings of anger, anxiety, activation, or unpleasantness during the neutral condition (ps > .10). However, non-parametric analyses using the Kruskal-Wallis H-test revealed a significant difference between subgroups in the extent to which individuals felt activation during the scan, $H(3) = 9.67$, p = .02. Post-hoc analysis using Dunn's test for multiple comparisons revealed significant differences between Subgroup 1 (M = 0.42) and Subgroup 2 (M = 2.94), p = .01, and between Subgroup 2 (M = 2.94), and Subgroup 4 (M = 0.47), p = .01. This finding is consistent with analyses of the frequency of arousal words participants in used their self-reports of what they chose to imagine while in the scanner for both the parametric ($F(3, 16) = 5.43$, p = .01, η_p^2 = .50) and nonparametric tests ($H(3) = 8.94$, p = .03). The subgroups that differed in VAS ratings of activation also differed in the frequency of arousal words used in their self-reports.

Specifically, post-hoc analysis using Tukey's Honestly Significant Difference test revealed a marginal difference between Subgroup 1 (M = 0.80) and Subgroup 2 (M = 2.25), p = .07, and a significant difference between Subgroup 2 (M = 2.25), and Subgroup 4 (M = 0.17), p = .01. Dunn's post-hoc test for the non-parametric analysis similarly revealed a marginal difference between Subgroups 1 and 2 (p = .07) and a significant difference between Subgroups 2 and 4 (p = .003). These findings are consistent with recent evidence demonstrating that arousal is associated with neuro-modulatory changes in intrinsic network connectivity (e.g., higher levels of arousal are associated with increased connectivity within the salience network; Young et al., 2017). In the present analysis, Subgroup 1, which had lower average scores on our measures of activation and arousal, had no connectivity between subnetworks of SAL (note however, that Subgroup 4 also had low scores on both measures of arousal/activation but did have connectivity between subnetworks of SAL).

Analyses of the remaining measures collected in the experiment revealed a marginally significant difference between subgroups on the TAS-20 measure of alexithymia, $F(3, 20)$ = 2.76, p = .07, η_p^2 = .29. Post-hoc analysis using Tukey's Honestly Significant Difference test revealed that this effect is being driven a marginal difference between Subgroup 3 (M = 45.43), and Subgroup 4 (M = 36.29), p = .05. There were no differences between subgroups in emotional complexity scores as measured by the RDEES (p = .90). See Table 5 for results from all tests, as well as their nonparametric equivalents.

Table 5. Parametric (Fisher's *F*-test) and Nonparametric (Kruskal-Wallis *H*-test) Comparisons of Neutral Subgroups 1-4

Measure	Subscale	Parametric Test	Nonparametric Test
VAS	Anger	$F = 0.70$, $p = 0.56$	$H = 6.87$, $p = 0.08$
	Anxiety	$F = 0.98$, $p = 0.42$	$H = 2.03$, $p = 0.57$
	Activation	$F = 2.30$, $p = 0.11$	$H = 9.67$, $p = 0.02$
	Unpleasantness	$F = 0.98$, $p = 0.42$	$H = 6.30$, $p = 0.10$
TAS-20	Overall Score	$F = 2.76$, $p = 0.07$	$H = 6.27$, $p = 0.10$
	Difficulty Describing Feelings	$F = 0.92$, $p = 0.45$	$H = 3.97$, $p = 0.26$
	Difficulty Identifying Feelings	$F = 0.86$, $p = 0.48$	$H = 2.73$, $p = 0.44$
	Externally-Oriented Thinking	$F = 1.78$, $p = 0.18$	$H = 4.09$, $p = 0.25$
RDEES	Overall Score	$F = 0.19$, $p = 0.90$	$H = 0.66$, $p = 0.88$
	Range	$F = 1.47$, $p = 0.25$	$H = 3.92$, $p = 0.27$
	Differentiation	$F = 0.39$, $p = 0.76$	$H = 1.11$, $p = 0.78$
Self-reported descriptions of what participants chose to think about while in the scanner	Frequency of Emotion Words Used	$F = 0.89$, $p = 0.47$	$H = 2.35$, $p = 0.50$
	Frequency of Valence Words Used	$F = 1.31$, $p = 0.31$	$H = 3.31$, $p = 0.35$
	Frequency of Arousal Words Used	$F = 5.43$, $p = 0.01$	$H = 8.94$, $p = 0.03$
	Frequency of Body Words Used	$F = 0.04$, $p = 0.99$	$H = 0.14$, $p = 0.99$
	Internal v. External Scenario	$F = 0.23$, $p = 0.87$	$H = 0.86$, $p = 0.84$
	Social vs. Nonsocial Scenario	$F = 0.68$, $p = 0.58$	$H = 1.78$, $p = 0.62$
	Remembered v. Imagined Scenario	$F = 1.00$, $p = 0.43$	$H = 3.00$, $p = 0.40$

Comparison to previous subgroups. Of most interest to the present study is the comparison of the neutral subgroups to those revealed during the anger and anxiety conditions. Although the neutral music task is similar to the anger and anxiety conditions in that participants were listening to music, the subgrouping procedure revealed different subgroups of individuals

than those in the two emotion induction conditions (See Figure 8). However, individuals did not differ in VAS ratings of emotion felt during the task, nor were there substantial differences in individual difference measures of emotion (no difference in RDEES scores and only a marginally significant difference between two subgroups in TAS-20 scores). One notable difference between the neutral subgroups and those revealed during the anger and anxiety condition is the greater degree (i.e., higher number of paths) of connectivity across networks.

Greater degree of connectivity for the neutral subgroups as compared to the anger and anxiety subgroups suggests degeneracy in cognitive processing that is related to factors not measured during the present experiment. This finding may also be consistent with growing evidence that neural networks are dynamically reconfigured to meet task demands (see Shine & Poldrack, 2018 for a review). For example, engaging in high-level construal results in global integration of networks (e.g., greater connectivity across distant nodes) as compared to low-level construal, which results in segregation of networks (e.g., greater connectivity between neighboring nodes; Stillman, Lu, & Fujita, 2020). Because there were fewer constraints imposed on participants during the neutral condition (i.e., they were not required to cultivate an emotional experience) it is plausible that they were engaging in higher level construal as compared to when they completed the emotion induction conditions, which required them to recall or imagine specific events in order to induce a particular emotion. Thus, it is possible that greater between-network connectivity in the neutral condition is a result of the level of construal required by the task. Further, the unconstrained nature of the task may have facilitated more mind-wandering or other cognitive processes extraneous to the music listening task. Ultimately, these findings show further evidence that the subgrouping procedure is not selecting on stable individual differences, but rather demonstrating the presence of degeneracy in the brain basis of emotion experience.

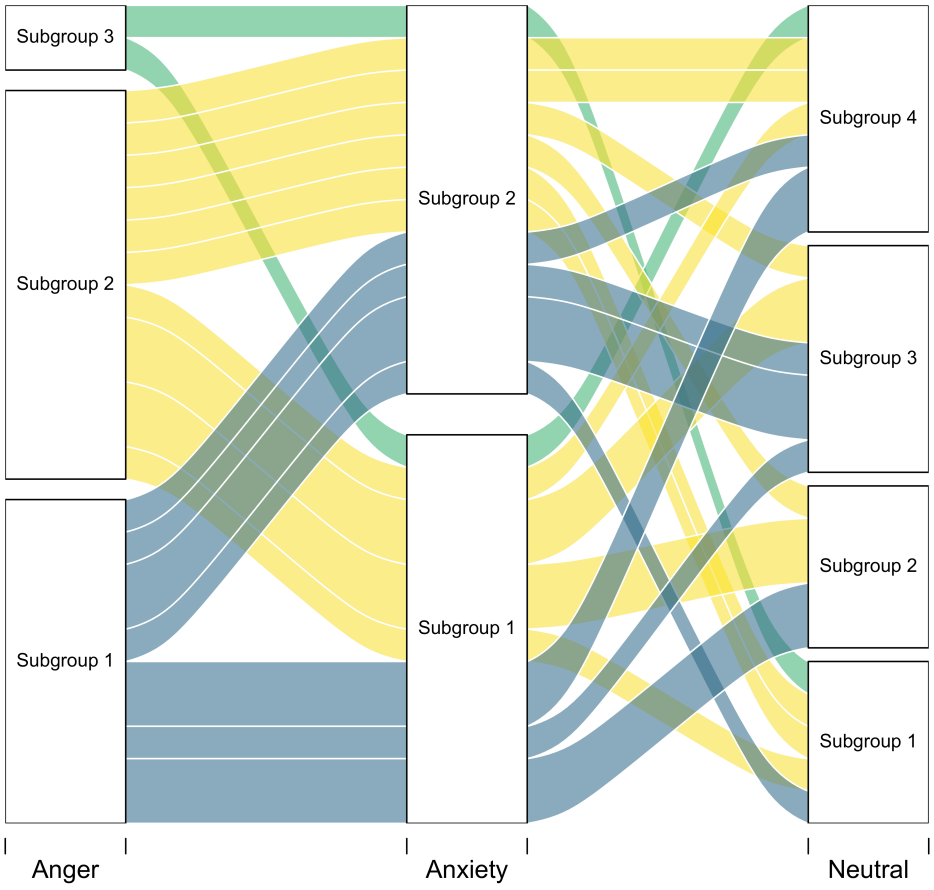


Figure 8. Subgroup membership across anger, anxiety, and neutral conditions. Subgroup classification during the neutral condition differed from that of the anger and anxiety conditions. These findings suggest that the subgroups revealed during the anger and anxiety conditions are the result of the evoked states rather than stable individual differences that would also be present during a task-positive control condition.

CHAPTER 6: ANALYSIS 4 – USING A TASK-NEGATIVE CONTROL CONDITION TO RULE OUT THE POSSIBILITY THAT SUBGROUPS WERE DETERMINED BY INDIVIDUAL-LEVEL FACTORS

As a final analysis step, I implemented the S-GIMME procedure on the resting state scan collected at the beginning of the fMRI experiment to investigate whether subgroups also emerge during a task-negative state. The purpose of this analysis is to provide additional evidence to rule out the possibility that the subgrouping procedure is selecting on stable individual differences that would also be present at rest.

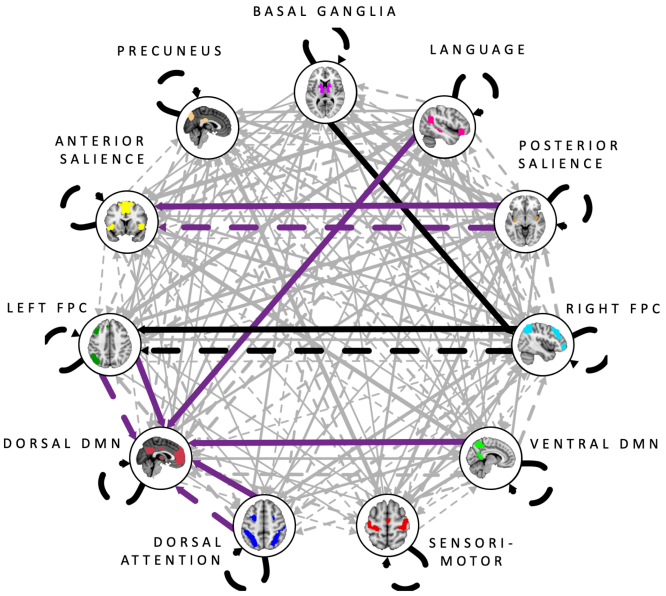
The resting state scan provides a task-negative control condition because participants were asked to simply lie at rest without listening to music or generating an emotional experience. I predicted that for the resting state scan, GIMME would reveal patterns of brain activation that correspond to typical resting state functional connectivity (e.g., connectivity within Shirer et al.'s subnetworks of the DMN and PCUN). In terms of the subgrouping procedure, I predicted that any subgroups revealed would reflect normal variability that occurs during task-negative states (e.g., variation in the configuration of the default mode network; Deco, Jirsa, & McIntosh, 2011; Deco et al., 2009). Finally, I predicted that resting state subgroups, if revealed, would be distinct from subgroups revealed for the previous analyses. Confirmation of these hypotheses would bolster the existing evidence for degeneracy in the brain basis of emotion experience.

Analysis 4: Resting State

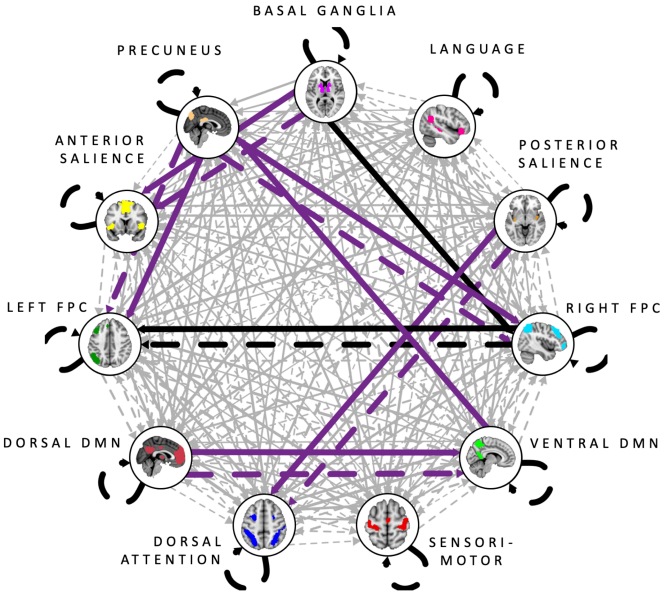
To conduct this analysis, I implemented the S-GIMME procedure on the time series from the resting state scan. For any subgroups revealed, I visually assessed differences in the presence v. absence of paths between networks during rest. VAS ratings and post-scan self-reports were

not collected for the resting state scan. However, I was able to compare subgroups revealed during rest based on the individual difference measures of emotional complexity (RDEES) and alexithymia (TAS-20) collected during the experiment. Finally, I again assessed the extent to which the subgroups revealed during rest differed from those revealed during the anger, anxiety, and neutral conditions.

Subgroup connectivity. S-GIMME revealed two subgroups of individuals based on their connectivity patterns during the resting state scan. Subgroup 1 (N = 6) had connectivity between subnetworks of DMN (from vDMN to dDMN) as well as from Lang to dDMN. However, Subgroup 1 did not have subgroup-level connectivity between PCUN and either of the subnetworks of DMN, suggesting less overall connectivity within DMN. Subgroup 2 (N = 18) had connectivity between subnetworks of DMN (from dDMN to vDMN), as well as from vDMN to PCUN. Subgroup-level connectivity maps for Subgroups 1 and 2 are depicted in Figure 9.



Subgroup 1



Subgroup 2

Figure 9. Subgroup-level connectivity maps for resting state. S-GIMME revealed two subgroups of connectivity patterns during resting state. Solid lines represent contemporaneous relationships and dashed lines represent lagged (X at time-1 predicts Y at time) relationships. Autoregressive paths (X at time-1 predicts X at time) appear as dashed loops. Contemporaneous group-level paths (black) from BG to rFPC, and contemporaneous and lagged group-level paths from rFPC to lFPC were significant for at least 75% of individuals across subgroups. All subgroup-level paths (purple) were significant for at least 75% of individuals within each subgroup. Individual-level paths (gray) represent each path that exists for at least one individual within the subgroup.

Music training and demographic measures. I again assessed whether subgroups differed in terms of age, sex, or years of music training. A Student's *t*-test revealed that Subgroup 1 (M = 2.33) and Subgroup 2 (M = 4.61) did not significantly differ in number of years of music training (p = .27). Similarly, a Student's *t*-test revealed that Subgroup 1 (M = 20.83) and Subgroup 2 (M = 23.61) did not significantly differ in age (p = .27). Finally, a Pearson's Chi-square test for independence with Yates' continuity correction revealed that subgroup classification was independent of sex, $\chi^2\ (1, N = 24) = 0.00,\ p = 1.00$. I next assessed whether there were any significant differences in the post-scan measures of interest.

Post-scan measures. Because the resting state scan did not involve music or an emotion induction task, participants did not complete the VAS ratings of anger, anxiety, unpleasantness, or activation after the scan. For the same reason, I did not collect self-reported descriptions of what participants chose to imagine while in the scanner. I was thus unable to assess any potential differences in these features of participants' experiences. I did, however, use Student's t-tests to assess differences between the subgroups on the other post-scan measures collected. These tests revealed no differences between subgroups in emotional complexity as measured by scores on the RDEES (p = .86), as well as no differences between subgroups on the TAS-20 measure of Alexithymia (p = .62). See Table 6 for results from all tests, as well as their nonparametric equivalents.

Table 6. Parametric (Student's *t*-test) and Nonparametric (Mann-Whitney *U*-test) Comparisons of Resting State Subgroups 1 and 2

Measure	Subscale	Parametric Test	Nonparametric Test
TAS-20	Overall Score	$t = 0.51$, $p = 0.62$	$U = 59$, $p = 0.76$
	Difficulty Describing Feelings	$t = -0.06$, $p = 0.95$	$U = 55$, $p = 0.97$
	Difficulty Identifying Feelings	$t = -0.11$, $p = 0.92$	$U = 55$, $p = 0.97$
	Externally-Oriented Thinking	$t = 1.01$, $p = 0.35$	$U = 70$, $p = 0.30$
RDEES	Overall Score	$t = -0.18$, $p = 0.86$	$U = 52.5$, $p = 0.95$
	Range	$t = -0.51$, $p = 0.62$	$U = 45.5$, $p = 0.59$
	Differentiation	$t = 0.12$, $p = 0.91$	$U = 61.5$, $p = 0.64$

Note: VAS ratings and self-reported descriptions of what participants thought about while in the scanner were not collected for the resting state scan

Comparison to previous subgroups. The subgroups revealed during the resting state scan were distinct from those revealed during the neutral condition, as well as those revealed during the two emotion induction conditions (See Figure 10). As might be expected, both subgroups revealed during the resting state scan exhibited different sub-configurations of canonical resting state connectivity (i.e., activity within the default mode network; Raichle et al., 2001). However, the fact that two subgroups were revealed during rest may reflect individual differences in resting state functional connectivity that are obscured when only considering mean-level activation. The subgroups revealed may again reflect degeneracy in cognitive processing that is related to factors not measured during the present experiment. Nonetheless, the finding that these subgroups differ from those revealed during other conditions provides further evidence that the subgrouping procedure is selecting on degenerate patterns of connectivity related to the experience of emotion.

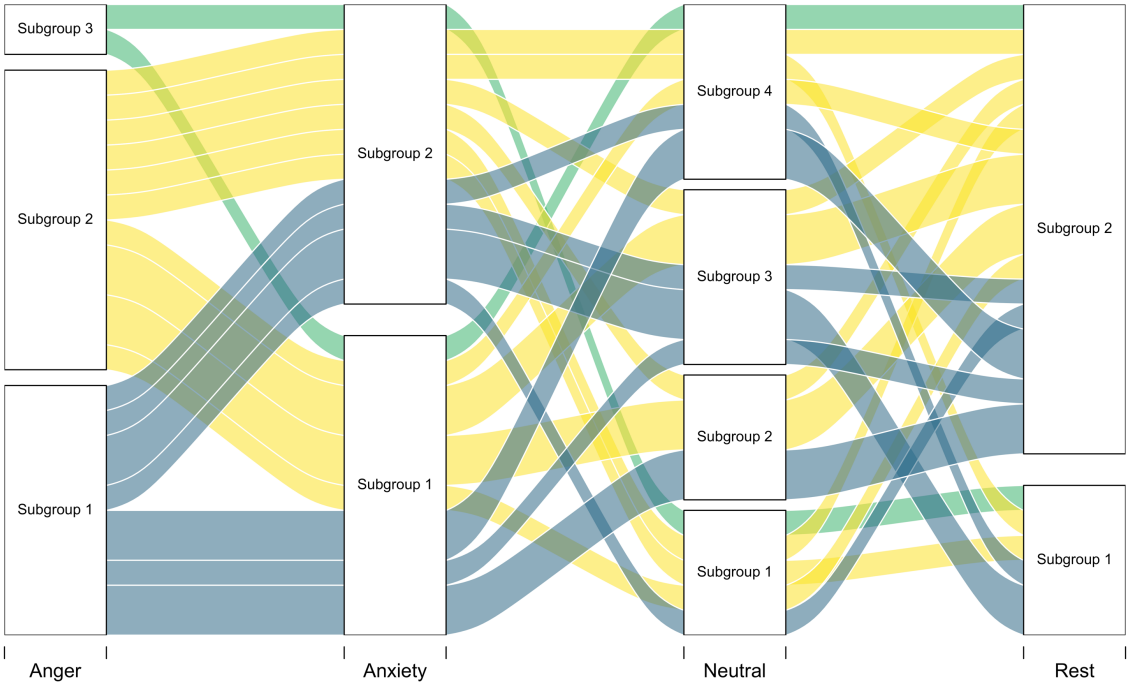


Figure 10. Subgroup membership across anger, anxiety, neutral, and resting state. Subgroup classification during resting state differed from that of the neutral condition as well as the anger and anxiety conditions. These findings demonstrate that the subgroups revealed during the anger and anxiety conditions are the result of the evoked states rather than stable individual differences that would also be present during task-positive or task-negative control conditions.

CHAPTER 7: REMAINING QUESTIONS

This project is a promising first step toward demonstrating the extent to which the experience of emotion is characterized by degeneracy. It employed a novel data-driven model selection algorithm to identify subgroups of individuals who have similar patterns of brain activation during the experience of emotion. However, there are several alternate hypotheses for the basis of the subgroups revealed in the present study. While some alternate hypotheses must be tested in future research, several can be tested with the data presently available. In this chapter, I will address three remaining questions regarding the nature of the subgroups: 1) is subgroup membership related to differences in degree of connectivity for individuals who scored higher v. lower on alexithymia? 2) is subgroup membership related to counterbalanced run order? 3) is subgroup membership related to subject head motion?

Is subgroup membership related to degree of connectivity in alexithymia?

The first remaining question involves whether the degree of connectivity underlying participants' emotional experiences contributed to subgroup membership over and above the individual difference measure of alexithymia. In three out of four conditions in the present study, I observed differences across subgroups in scores on the TAS-20 measure of alexithymia (i.e., anger, anxiety, and neutral). It is possible that the subgroups revealed also differed in degree of individual-level connectivity based on whether they scored higher v. lower on the TAS-20 measure. If the subgroups with higher alexithymia scores also had greater degree of connectivity, it would leave open the possibility that subgroup membership is simply based on the number of paths between networks, rather than differences in the features of participants' experiences. To

test for subgroup differences in degree of connectivity, I computed the number of paths in each participant's individual-level connectivity map for each of the three conditions. Within each condition, I compared average degree of connectivity between the two subgroups that differed on the TAS-20 measure of alexithymia.

Anger Condition. Participants in Subgroup 1 contained participants who scored, on average, higher on the TAS-20 (M = 44.20) as compared to participants in Subgroup 2 (M = 37.67), $t(18.99) = 2.51$, $p = .02$, Cohen's $d = 1.04$, 95% CI [0.08, 1.99]. However, there was no difference in average degree of connectivity for participants in Subgroup 1 (M = 43.70 paths) and Subgroup 2 (M = 43.92 paths), $p = .94$.

Anxiety Condition. Participants in Subgroup 1 scored higher on the Difficulty Identifying Feeling (DIF) Subscale of the TAS-20 (M = 15.33) as compared to participants in Subgroup 2 (M = 12.00), $t(21.47) = 2.30$, $p = .03$, Cohen's $d = .94$, 95% CI [0.05, 1.83]. As with the anger condition, however, there was no difference in average degree of connectivity for participants in Subgroup 1 (M = 41.83 paths) and Subgroup 2 (M = 45.92 paths), $p = .20$.

Neutral Condition. An analysis of variance revealed a marginal difference between subgroups on the TAS-20 measure of alexithymia, $F(3, 20) = 2.76$, ($p = .07$), $\eta_p^2 = .29$. Post-hoc analysis using Tukey's Honestly Significant Difference test revealed that this effect was driven a marginal difference between Subgroup 3 (M = 45.43), and Subgroup 4 (M = 36.29), $p = .05$. However, consistent with my analyses of the emotion induction conditions, there was no difference in average degree of connectivity for participants in Subgroup 3 (M = 27.29 paths) and Subgroup 4 (M = 31.00 paths), $p = .47$.

The above analyses demonstrate that the subgroups revealed during the anger, anxiety, and neutral conditions were not merely the result of differences in degree of connectivity related

to higher scores on the TAS-20 measure of alexithymia. This is perhaps because alexithymia has been associated with diminished connectivity within the DMN, and simultaneously greater connectivity between DMN and areas involved in sensory input and cognitive control (Liemburg, Swart, Bruggeman, Kortekaas, & Knegtering, 2012; Moriguchi & Komaki, 2013). Put differently, overall degree of connectivity may not differ across these subgroups because decreased connectivity within self-referential regions of the brain in alexithymia may be canceled out by greater connectivity elsewhere. Nonetheless, these findings suggest that the subgroups revealed in the present study are associated with the features of participants' experiences rather than the degree of connectivity underlying those experiences.

Is subgroup membership related to counterbalanced run order?

The second remaining question involves whether the subgroups identified in the present experiment depended on the order in which participants completed the within-subjects emotion induction conditions. The scan procedure involved counterbalancing the order in which participants engaged in the anger and anxiety inductions, so it is possible that participants' experiences may have differed depending on whether they completed the anger condition first or the anxiety condition first. For example, completing the anxiety condition first could have had a residual effect on the anger condition such that those participants' angry brain states looked different from "pure" angry states, and vice versa. To assess this possibility, I conducted Chi-square analyses for both the anger and anxiety conditions to test for independence between subgroup membership and counterbalanced run order.

Anger Condition. Pearson's Chi-square test for independence with Yates' continuity correction revealed that subgroup classification during the anger condition was independent of

whether participants completed the anger induction before or after completing the anxiety induction, $\chi^2\ (1, N = 22) = 0.002,\ p = 0.97$.

Anxiety Condition. Pearson's Chi-square test for independence with Yates' continuity correction revealed that subgroup classification during the anxiety condition was independent of whether participants completed the anxiety induction before or after completing the anger induction, $\chi^2\ (1, N = 24) = 0.00,\ p = 1.00$.

The above analyses demonstrate that subgroup membership in the anger and anxiety conditions is independent of counterbalanced run order. Thus, I can rule out the alternate explanation that the counterbalanced order in which participants completed the within-subjects conditions shaped their experiences in ways that determined their subgroup membership.

Is subgroup membership related to head motion?

The final remaining question that can be answered with the available data is whether subgroup membership is related to differences in head motion during the experiment. The data collected in the present experiment were censored for head motion using the ART toolbox. ART identifies timepoints with excessive motion and uses them as nuisance regressors in the first-level analysis step. Despite the implementation of this procedure, however, it remains possible that motion artifacts still contributed to the findings. Because head motion mimics functional connectivity (Power, Barnes, Snyder, Schlaggar, & Petersen, 2012), it is critical to rule out the alternate hypothesis that subgroup classification in the present study was influenced by motion artifacts. As a conservative test of whether there were differences in motion across the subgroups revealed, I conducted a separate analysis of subgroup differences in head motion prior to the implementation of the ART procedure.

Following Van Dijk, Sabuncu, and Buckner (2012), I computed mean and max displacement for each participant as the root mean square (RMS) of the translation parameters such that $displacement = sqrt(x^2 + y^2 + z^2)$. I then assessed whether there were differences between subgroups in the mean and max displacement metrics.

Anger Condition. There were no differences between Subgroup 1 (M = .133 mm) and Subgroup 2 (M = .139 mm) in mean displacement during the anger condition, p = .79. Similarly, there were no differences between Subgroup 1 (M = .398 mm) and Subgroup 2 (M = .635 mm) in max displacement during the anger condition, p = .41.

Anxiety Condition. There were no differences between Subgroup 1 (M = .145 mm) and Subgroup 2 (M = .176 mm) in mean displacement during the anxiety condition, p = .30. Similarly, there were no differences between Subgroup 1 (M = .693 mm) and Subgroup 2 (M = .787 mm) in max displacement during the anxiety condition, p = .75.

Neutral Condition. There were no differences between Subgroup 1 (M = .134 mm), Subgroup 2 (M = .149 mm), Subgroup 3 (M = .135 mm), and Subgroup 4 (M = .134 mm) in mean displacement during the neutral condition, p = .40. Similarly, there were no differences between Subgroup 1 (M = .502 mm), Subgroup 2 (M = .695 mm), Subgroup 3 (M = .362 mm), and Subgroup 4 (M = .339 mm) in max displacement during the neutral condition, p = .18.

Resting State. There were no differences between Subgroup 1 (M = .139 mm) and Subgroup 2 (M = .142 mm) in mean displacement during resting state, p = .91. Similarly, there were no differences between Subgroup 1 (M = .437 mm) and Subgroup 2 (M = .727 mm) in max displacement during resting state, p = .32.

In sum, there were no differences between subgroups in mean or max displacement during any of the four within-subjects conditions. I can thus rule out the alternate explanation

that the subgroups revealed in the present study are the result of motion artifacts. Together, the findings from these three additional analyses help to rule out the alternate hypothesis that the subgroups revealed during the anger and anxiety conditions are a result of noise or some other factor unrelated to the experience of emotion. Rather, these subgroups represent initial evidence for between-person degeneracy in the experience of anger and anxiety.

CHAPTER 8: GENERAL DISCUSSION

This work is the first to empirically investigate the principle of degeneracy in the brain basis of emotion experience. I predicted and found that across participants, different neural pathways can produce the same category of emotional experience. During the experience of anger and anxiety, subgroups of individuals had emotional experiences that differed in terms of the features of that category, but not in the category experienced itself.

In my first analysis, S-GIMME revealed two subgroups approximating the experimental conditions participants completed. This finding suggests that the algorithm was selecting on variability related to differences in the experiences of anger and anxiety participants generated in the scanner. However, I also found a third subgroup which contained brain states from both the anger and anxiety conditions. This is interesting because it suggests that some features of the neural representations of anger and anxiety are shared across both experiences. The finding that there was not perfect segregation of experimental conditions is consistent with the psychological constructionist view that emotions are not characterized by specific "neural signatures." Rather, the experience of emotion is represented in distributed brain regions and networks that support psychological processes that are not themselves unique to emotion (see Barrett, 2017). Thus, it is not surprising that some brain states associated with anger and anxiety were classified into the same subgroup.

My primary hypothesis was that there would be degeneracy within instances of anger and anxiety. The results from my second analysis supported this hypothesis. Participants in both of

the anger subgroups experienced the same degree of anger, despite the fact that Subgroup 1 experienced anger as a slightly more unpleasant state. Subgroup 1 also scored higher on alexithymia, a subclinical emotional disorder that has been linked to the experience of greater intensity of negative affect (Byrne & Ditto, 2005; Friedlander et al., 1997; Luminet et al., 2004). In terms of connectivity patterns, Subgroup 1 was characterized by greater connectivity within subnetworks of the salience network. These findings converge nicely with prior work showing that activation within regions of the salience network is associated with the experience and intensity of negative affect (Lindquist et al., 2016; Seeley et al., 2007; Touroutoglou, Hollenbeck, Dickerson, & Barrett, 2012b). On the one hand, it may be tempting to conclude that individuals who were experiencing anger that was more intensely negative were experiencing a categorically different state. However, there is substantial variability within an emotion category in terms of the features that are experienced. Although it is commonly assumed that each emotion category is characterized by a prototypical degree of valence and activation, in actuality, there is substantial variance in how unpleasant or activating any given instance of an emotion category is experienced to be (Kuppens, Tuerlinckx, Russell, & Barrett, 2013; Kuppens et al., 2017; Wilson-Mendenhall, Barrett, & Barsalou, 2014). Thus, it is reasonable to assume that participants were experiencing instances of anger with slightly different features; the subgroups revealed in the present study seemed to reflect these distinctions.

As with the anger condition, participants in both of the anxiety subgroups experienced the same degree of anxiety (note that the parametric—but not the nonparametric—analysis of VAS ratings of anxiety revealed a significant difference in reported anxiety prior to the removal of one outlier that was having undue leverage on the results). Subgroup 1 contained individuals who scored higher on the Difficulty Identifying Feelings (DIF) subscale of the TAS-20. This same

subgroup was also characterized by less connectivity between the language network and the left frontoparietal control network. Lack of connectivity between these networks may explain Subgroup 1's higher scores on the DIF subscale of the TAS-20 insofar as decreased connectivity within these networks reflects difficulty in semantic selection and retrieval that is necessary to identify and label one's emotional state (Chiou, Humphreys, Jung, & Lambon Ralph, 2018; Hirshorn & Thompson-Schill, 2006; Klein, Milner, Zatorre, Meyer, & Evans, 2006; Whitney, Kirk, O'Sullivan, Lambon Ralph, & Jefferies, 2011). Unlike the anger condition, participants did not appear to differ in any of the qualitative features of anxiety, as assessed by VAS scores or open-ended reports.

The findings from the anger and anxiety conditions suggest degeneracy in the brain basis of emotion experience. However, those findings alone are unable to fully rule out the alternate hypothesis that the observed subgroups refelct person-level factors that are unrelated to the evoked anger and anxiety states. I thus conducted two additional analyses afforded by the experimental design—one of a task-positive control condition (neutral), and one of a task-negative control condition (resting state). My analysis of the neutral condition revealed four subgroups of individuals. Those subgroups collectively exhibited a greater degree of connectivity (i.e., total paths between networks) compared to the subgroups revealed during the anger and anxiety conditions. This increase in degree of connectivity between networks may reflect the unconstrained nature of the task, as greater global connectivity has been associated with tasks that involve a more expansive scope (i.e., higher level of construal; Stillman et al., 2020). Importantly, the four subgroups revealed during the neutral condition were similar in their reports of what they experienced during the scan, except that they differed in the degree to which they felt activation during the task and used more arousal-related words to describe what they

chose to imagine in the scanner. They also differed only slightly in the individual difference measures collected following the experiment (i.e., one marginally significant difference in TAS-20 scores between Subgroups 3 and 4). Critically, consistent with my hypothesis, the subgroups revealed during the neutral condition were distinct from those revealed during the anger and anxiety conditions. These findings provide further evidence that the subgroups revealed during the evoked anger and anxiety states were not a result of stable person-level factors that would be present during an affectively neutral, task-positive control condition.

As a final analysis step, I implemented the S-GIMME procedure on the resting state data collected at the beginning of the experiment. The purpose of this step was to provide the most stringent test of the alternate hypothesis that the subgroups revealed during the anger and anxiety conitions are the result of stable person-level factors that would also be present during a task-negative control condition. Analysis of the resting state data revealed two subgroups of individuals. Both subgroups exhibited patterns of connectivity that would be expected during rest. Specifically, Subgroup 1 had connectivity between subnetworks of default mode and between the default mode and the language network, whereas Subgroup 2 had connectivity between subnetworks of default mode and the precuneus network. The subgroups revealed during rest likely reflect two sub-configurations of the default mode network, as prior work shows that the canonical default mode network can be fractionated into subnetworks. For instance, the medial aspects of the default mode network (containing the precuneus) can be differentiated from the lateral language areas and the angular gyrus (Yeo et al., 2011). The precuneous is associated with memory and self-relevant visual imagery (Cavanna & Trimble, 2006) whereas the language network is associated with semantic processing (Demonet et al., 1992). These networks may thus reflect people who are in relatively different “modes” of the

default state, such as mind-wandering that is relatively more autobiographical/imagery-based v. mind wandering that is more semantic and linguistic. It would be interesting to investigate this finding in future research. Most critically, the subgroups revealed during rest are distinct from those revealed during the anger, anxiety, and neutral conditions.

Taken together, the findings observed in the present study suggest degeneracy in the brain basis of emotion experience. Evidence for degeneracy in the distributed patterns of brain activation during the experience of emotion is ultimately consistent with the Theory of Constructed Emotion (TCE), which proposes that emotions are variable populations of instances that arise from combinations amongst a set of domain-general intrinsic networks (Clark-Polner et al., 2017; Touroutoglou et al., 2015; Wager et al., 2015; see Barrett & Satpute, 2013 for a review). These findings add to growing evidence that the brain processes associated with different emotion categories are not as categorical as typically assumed (Lindquist et al., 2012; Wilson-Mendenhall, Barrett, Simmons, & Barsalou, 2011). For instance, the amygdala is involved in almost every type of emotion experience and perception—not just the category of fear. The brain states associated with emotion experience are characterized by between-category variation, but critically, also by important within-category variation (Leshin, McCormick, Doyle, Nam, & Lindquist, *in prep*; Wang, Boatman, & Satpute, *in prep*; Wilson-Mendenhall et al., 2014). This within-category variation corresponds to differences in the situated behaviors, sensations, and phenomenology that people experience across different instances of the same emotion.

Emotions are situated conceptualizations that are tailored to the immediate environment (Barrett & Lindquist, 2008). As such, the features that make up an emotion category are thought to vary across contexts. The present work revealed some evidence that the features of an emotion

experience may vary, although questions remain about what those features might be. Nonetheless, it is possible that those features contributed to the subgroups observed. However, to the extent that one might subscribe to the idea that emotion categories should be fractionated into subtypes (Adolphs, 2017; Scarantino, 2009; Silva et al., 2013), it could be argued that the subgroups revealed simply represent different subtypes of the same emotion (e.g., social fear v. fear of a predator). Future research would be needed to rule out this alternate explanation, and would require conducting the same experiment across multiple samples or within the same sample across time. If the same connectivity patterns were to appear across multiple samples or within the same sample across time, it would suggest that these subgroups reflect subtypes of the same emotion (i.e., Subgroups 1 and 2 from the anger condition reflect two distinct subtypes of anger). However, if there are differences in connectivity patterns across samples or across time during the experience of the same emotion, it would provide evidence for degeneracy in the brain basis of emotion experience. The latter would most likely be the case, as there is probably more variability in emotion experience than can be captured by a select group of emotion subtypes. If variability in emotion is linked to situational context, then there would be as many emotion "subtypes" as there are situations.

The idea that emotions vary based on situational context underscores why degeneracy in brain function likely exists. Manipulating the situational context surrounding an affective experience alters the distributed patterns of neural activation underlying that experience. For instance, emotions such as anger and fear are represented differently when experienced in a physical danger situation vs. a social evaluation situation (Wilson-Mendenhall et al., 2011). The present research adds to growing evidence that emotions are not biologically determined responses with stable neural signatures, but rather situated conceptualizations with distributed

neural representations that vary across individuals. Within-category variation, and corresponding neural degeneracy, even exists within the relatively more constrained adaptive behavioral responses that non-human animals engage in (Barrett & Finlay, 2019).

Limitations and Caveats

There are several limitations and caveats of the present research. First, this study was limited by a small sample size, as has traditionally been common in neuroimaging research. However, my analytic approach relies on the uSEM framework, in which time points—rather than participants—serve as sampling units. In the present study, each participant has 150 time points per run, and simulations show that S-GIMME can recover reliable subgroups with as few as 60 timepoints (Lane et al., 2019). Thus, I was well-powered to detect subgroups if they existed using S-GIMME. I may have been underpowered to find differences in behavioral or self-report data that characterized those subgroups, however. Future studies might use a larger sample size to see if the general pattern observed here replicates.

A second limitation is related to the emotion induction method employed in the present experiment. While the continuous music technique is a well-established method for reliably and robustly inducing emotion (Eich, 1995), it affords researchers little control over the content of participants' emotional experiences in the scanner. It is (perhaps erroneously) assumed that there is more homogeneity in the processes invoked via visual methods of emotion induction (e.g., viewing slides from the International Affective Pictures System; Lang, Bradley, & Cuthbert, 2008), yet this is ultimately an empirical question. A meta-analysis of emotion induction techniques found that the effect size associated with viewing pictures was large (Hedges' g = .81), whereas the effect size associated with imagination or music inductions were considered medium (Hedges' g = .51 and .53, respectively; Lench, Flores, & Bench, 2011). However, tasks

that induce emotion in the scanner using aversive images lack ecological validity and idiographic richness. The emotion induction task used in the present study may actually be a strength for addressing degeneracy because it required participants to self-generate actual or prospective scenarios and to experience the features of the emotion category that they find most personally relevant to the prescribed emotion. Nonetheless, it would be important to see if degeneracy in emotional brain states occurs across different induction methods, including those that might produce more heterogenous brain states.

A third limitation of the present research is that the subgroup differences revealed may reflect unmeasured processes rather than degeneracy in emotion experience *per se*. For instance, it is possible that the subgroups revealed in the present study reflect differences in the extent to which participants may have engaged in emotion regulation or allowed their minds to wander during the task. It is also possible that these subgroups reflect differences in strategies participants used to cultivate emotional experiences (e.g., differences in the types of scenarios that participants simulated during the emotion induction tasks) that are peripheral to the emotion being experienced. The lack of meaningful differences in self-reports of what participants chose to imagine while in the scanner suggests that this is not the case. However, I cannot fully rule out the possibility that I failed to detect such differences because participants were simply not asked the right questions, and that collecting additional self-report measures may have revealed those differences. Especially with regard to the question about emotion regulation, future research might address the extent to which participants were explicitly trying to reduce the intensity of their unpleasant feelings during the task.

A final caveat of the present research is that I chose one set of network-based ROIs to guide my approach. There are multiple parcellations of intrinsic networks available in the

literature, including those that prioritize temporal segregation v. those that prioritize spatial segregation of brain structures (Smith et al., 2012). I opted for the Shirer et al. (2012) ROIs because their multiple networks offered a level of granularity that would allow me to assess connectivity between multiple networks during emotion rather than merely focusing on one or two networks, as in past work (e.g., Raz et al. 2012; 2016). The Shirer et al. (2012) parcellation includes 90 functional ROIS comprising 14 intrinsic networks known to be involved in emotion. These ROIs were derived during rest and validated through classification of three subject-driven cognitive states. Because these ROIs outperformed existing structural ROIs in terms of their classification accuracy (Shirer et al., 2012), I felt they were appropriate for use in the present study.

One potential drawback of the Shirer et al. (2012) ROIs is that certain regions fall into multiple networks. Perhaps most notably, the precuneus is a region in several of Shirer et al.'s (2012) functionally defined networks (e.g., both subnetworks of DMN, left FPC, posterior SAL, and of course PCUN). However, this partially overlapping network parcellation respects the functional architecture of the brain. Indeed, while canonical networks have been traditionally assumed to be constellations of mutually exclusive brain regions functioning in parallel, there is considerable overlap such that regions in association cortex belong to multiple networks (Najafi, McMenamin, Simon, & Pessoa, 2016; Xu et al., 2013; Yeo, Krienen, Chee, & Buckner, 2014). Moreover, this functional overlap is dynamic, such that brain regions are continually shifting network affiliation over time (Ciric, Nomi, Uddin, & Satpute, 2017). Such overlap is consistent with degeneracy's complimentary opposite—pluripotentiality—where a single brain region or structure can perform multiple functions (Noppeney et al., 2004). It would be interesting in

future work to examine the degree of consistency v. differentiation that is found in subgroups depending on the network configurations assessed.

Future Directions

The present work focused on degeneracy in the neural representation of emotion across individuals. However, findings from lesion studies, which demonstrate unimpaired affective functioning despite damage to limbic structures (e.g., Becker et al., 2012; Damasio, Damasio, & Tranel, 2013; Feinstein, 2013; Feinstein et al., 2016, 2010), suggest that degeneracy is also likely to occur within individuals. Future work should examine intra-individual degeneracy in neural network activity during emotional experience. For instance, this could be achieved by conducting multiple-session experiments in which participants complete the same emotion task across at least two time points. A study designed to investigate intra-individual degeneracy should differ from typical longitudinal designs in that sessions should be linked closely in time (e.g., within the same day or separated by only a few days) in order to preclude the possibility that intra-individual changes in neural activation during the same task across scans is a result of typical developmental changes in functional connectivity that occur across time. If the same individuals are found to cluster into the same subgroups across time, it would mean that the subgroups might represent subtypes of the given emotion category. Alternatively, if subgroups differ across time, not only in their composition but also in the constellations of connectivity they represent, it would provide evidence for intra-individual degeneracy in the experience of emotion. This type of approach would also allow researchers to begin to home in on the extent to which stable individual differences v. situated variability contribute to degenerate brain states of emotion.

Finally, an obvious next step of this research program would be to examine how degeneracy is related to emotional dysfunction. It would be interesting to explore how intra-

individual degeneracy exists across people with and without emotion-based psychopathology. There is some evidence that variation in functional connectivity is adaptive for network function (Deco et al., 2009; Ghosh, Rho, McIntosh, Kötter, & Jirsa, 2008; McDonnell & Ward, 2011) and is related to cognitive flexibility (Cohen, 2018). Thus, individuals with psychopathology may have less neural degeneracy. Finding that degeneracy is associated with adaptive cognitive and emotional functioning would provide further evidence for the importance of studying individual differences in network connectivity. This research would be an important first step toward understanding factors that predict variability in the extent to which intra-individual degeneracy exists in the brain basis of emotion experience.

Conclusion

Recent methodological advances in neuroscience have enabled researchers to study emotions as dynamic, contextualized experiences (Barrett & Satpute, 2017), an approach that is more consistent with the emerging scientific picture of the nature of emotion. This work contributes to this movement by applying a novel unsupervised classification algorithm to investigate the principle of degeneracy in emotional experience across individuals. The S-GIMME algorithm enabled me to investigate individual-level differences that traditional neuroimaging analyses do not allow. These findings suggest that patterns of neural activation during emotion experience are characterized by considerable degeneracy across individuals. Although generally well-accepted in the biological sciences, the notion of degeneracy in the brain basis of emotion experience is just beginning to take hold. I hope that these findings will help set the stage for future research examining degeneracy in processes related to emotion and beyond.

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