

Variety in emotional life: within-category typicality of emotional experiences is associated with neural activity in large-scale brain networks

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The tremendous variability within categories of human emotional experience receives little empirical attention. We hypothesized that atypical instances of emotion categories (e.g. pleasant fear of thrill-seeking) would be processed less efficiently than typical instances of emotion categories (e.g. unpleasant fear of violent threat) in large-scale brain networks. During a novel fMRI paradigm, participants immersed themselves in scenarios designed to induce atypical and typical experiences of fear, sadness or happiness (scenario immersion), and then focused on and rated the pleasant or unpleasant feeling that emerged (valence focus) in most trials. As predicted, reliably greater activity in the ‘default mode’ network (including medial prefrontal cortex and posterior cingulate) was observed for atypical (vs typical) emotional experiences during scenario immersion, suggesting atypical instances require greater conceptual processing to situate the socio-emotional experience. During valence focus, reliably greater activity was observed for atypical (vs typical) emotional experiences in the ‘salience’ network (including anterior insula and anterior cingulate), suggesting atypical instances place greater demands on integrating shifting body signals with the sensory and social context. Consistent with emerging psychological construction approaches to emotion, these findings demonstrate that it is important to study the variability within common categories of emotional experience.

Keywords: emotion; affective neuroscience; typicality

INTRODUCTION

In his late nineteenth century writing, William James emphasized the tremendous variability in the human emotions that people refer to with the same emotion word (James, 1890). Consider the emotion category *fear*. Feelings of *fear* can emerge when excitedly declaring a risky bet, when lethargically sensing the first signs of flu, when frantically fleeing a blazing fire, or when casually flirting with an attractive stranger. While psychologists often acknowledge that diverse emotional experiences exist, surprisingly little empirical work attempts to document and explain the variability within categories of emotion experience (cf. Smith and Kirby, 2009; Barrett, 2013).

In contrast to traditional ‘basic’ emotion views, which remain focused on identifying the biological signatures of five or so emotion categories (for a review, see Tracy and Randles, 2011), a psychological construction approach predicts that tremendous variety in emotional life exists because coordinated and interacting domain-general neural systems produce countless possible emotional experiences (Barrett, 2009b, 2013). The shift from focusing on what makes a category unique to understanding meaningful variance both within and across categories is not a new scientific story—it parallels an empirical shift that occurred in cognitive psychology several decades ago. The empirical discovery that some instances of a category are more typical than others challenged the classical view that a rule with necessary and sufficient conditions could distinguish a category from all others (Rosch, 1973; Rosch and Mervis, 1975). Typicality refers to how good of an example a particular instance is of its category. For example, *robin* is a more typical example of the category *bird* than

penguin, which is an atypical example (Rosch, 1973; Rosch and Mervis, 1975). If category membership is determined by a rule, then typicality gradients should not exist—every category member should be an equally good example of the category.

It is now well accepted that typicality gradients are a central and ubiquitous property of many different categories (Rips *et al.*, 1973; Rosch, 1973, 1975; Smith *et al.*, 1974). Typicality gradients are evident when participants explicitly rate category instances and when participants perform tasks that use more implicit dependent measures (e.g. reaction time) (Smith *et al.*, 1974; McCloskey and Glucksberg, 1979; Casey, 1992). Initial evidence suggests that typicality gradients also exist within emotion categories (e.g. *fury* is a more typical example of *anger* than *impatience* or *discontent*) (Fehr and Russell, 1984, 1991; Russell, 1991; Russell and Fehr, 1994). Despite this and other evidence of variability *within* emotion categories (e.g. Nezelek *et al.*, 2008; Kreibitz, 2010), neuroimaging studies rely almost exclusively on highly typical instances when investigating the neural bases of emotion categories such as fear, happiness and sadness.

To examine the variability within three common emotion categories, we systematically manipulated one property of emotional experiences: affective valence. The affective circumplex implies a one-to-one relationship between emotion categories and affective valence: fear and sadness are unpleasant, and happiness is pleasant (Barrett and Russell, 1998; Russell and Barrett, 1999). However, this organization is driven by very typical instances of these emotions. Less typical fear experiences, for example, are sometimes pleasant: the scary thrill of zipping downward on a rollercoaster or the jittery exhilaration of performing before a crowd. Less typical happiness experiences are sometimes unpleasant: the exhausting relief of finishing a time-consuming project or the freeing reprieve of a friend’s comforting words when distressed (i.e. when the relative shift toward feeling pleasant tends to make the feeling tone simply less unpleasant).

In this experiment, we investigated the neural correlates of valence-driven typicality gradients in three common emotion categories. Participants immersed in vividly imagined scenarios to induce fear,

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sadness, and happiness experiences. We initially examined typicality discretely, contrasting *typical* (i.e. more typical) emotional experiences involving the valence described within the affective circumplex (i.e. unpleasant fear, unpleasant sadness, pleasant happiness) with *atypical* (i.e. less typical) emotional experiences involving the opposite valence (i.e. pleasant fear, pleasant sadness, unpleasant happiness) (see Table 1 for examples). Because typicality is usually examined as a continuous gradient, and because, initially, we did not measure typicality directly (instead using valence as a proximate measure), we also collected typicality ratings of the scenarios from an independent sample. Examining the relationship between the typical-to-atypical gradients specified by the ratings and brain activity provided an additional, stringent test of our hypotheses.

During the fMRI experiment, participants immersed themselves in scenarios designed to induce various typical and atypical experiences of fear, sadness or happiness, which we will refer to as ‘scenario immersion’. On most trials, participants subsequently focused on and rated the pleasant or unpleasant feeling that emerged during immersion, which we will refer to as ‘valence focus’.¹ To facilitate immersion, participants received training on how to immerse themselves in richly detailed, full versions of the scenarios outside the scanner. This practice facilitated easily re-experiencing the scenarios during neuroimaging when prompted with shorter, core versions of the scenarios.

Because a psychological construction approach suggests that diverse emotional experiences are produced from the interplay of domain-general neural systems (Barrett, 2009a), we hypothesized that common neural circuitry would be engaged across the three categories of emotional experience. Coordinated, anatomically constrained brain networks are consistently identified using resting state methods (e.g. Yeo *et al.*, 2011) and appear to support basic operations central to constructing emotional experiences (Lindquist and Barrett, 2012; Barrett and Satpute, 2013). More specifically, we hypothesized that we would observe increased activity during the more atypical (*vs* typical) instances, across emotion categories, in large-scale networks that support processing during scenario immersion and during valence focus (which we describe in more detail below). Our assumption is that typical and atypical instances rely on these networks, but that atypical instances ‘drive’ these systems harder. In the same way that decreased neural activity in repetition suppression is interpreted as increased processing efficiency (Grill-Spector *et al.*, 2006), we propose that increased activity for atypical instances is interpreted as placing greater demands on the system, decreasing processing efficiency. This framework is consistent with the cognitive science literature showing that atypical instances tend to be learned at a slower rate and categorized less quickly than more typical instances (Smith *et al.*, 1974; McCloskey and Glucksberg, 1979; Casey, 1992; Larochelle and Pineau, 1994; Russell and Fehr, 1994).

During the scenario immersion phase, participants projected themselves into a situation in which bodily reactions were tied to an event in the world, producing an emotional experience. The ‘default mode’ network (DMN), with hubs in midline medial prefrontal cortex and posterior cingulate, plays a central role in emotional experiences (as revealed by recent meta-analyses; Lindquist *et al.*, 2012) and in many other kinds of experiences, including memory, self-evaluation, prospection, theory of mind, moral reasoning, and spontaneous thought (for reviews, see Buckner *et al.*, 2008; Schilbach *et al.*, 2008; Lindquist and Barrett, 2012; Mars *et al.*, 2012; Barrett and Satpute, 2013). Although initial thinking about the ‘common thread’ across these tasks involved self-referential processing (e.g. Northoff *et al.*, 2006),

recent reviews suggest that the DMN serves a broader role in the context-based, conceptual processing that occurs during complex categories of mental experience (e.g. emotions, beliefs and attitudes), which are dynamically constructed using prior experience to direct physiological, perceptual, and motor responding (e.g. Bar, 2007; Buckner and Carroll, 2007; Barrett, 2012; Lindquist and Barrett, 2012). The heteromodal regions that comprise the DMN appear well-suited to hierarchically integrate information across modalities and across time to produce inferences tailored to the socio-emotional situation (e.g. Krueger *et al.*, 2009). We predicted that atypical (*vs* typical) instances would be associated with heightened activity in the DMN, particularly during scenario immersion, due to the increased conceptual processing required to situate the atypical emotional experience.

Once immersed in a scenario, participants foregrounded the pleasant/unpleasant feeling evoked during the emotion induction so they could report it—the valence focus phase. The anterior cingulate and fronto-insular cortex hubs of the ‘salience’ network (SN) have been implicated in a variety of emotional experiences (both positive and negative) as well as other experiences involving subjective feelings of affect and agency (Craig, 2009; Laird *et al.*, 2011; Cauda *et al.*, 2012; Touroutoglou *et al.*, under review). Recent reviews suggest that this network integrates highly processed sensory information with somato-visceral information from the body to guide attention and decision-making (Menon and Uddin, 2010; Lindquist and Barrett, 2012; Barrett and Satpute, 2013). Because valence is the prominent feature that makes the instance atypical, we hypothesized that during atypical instances increased processing would be needed to integrate fluctuating body signals with the sensory and social context constructed during scenario immersion to report the subjective feeling. Due to these increased demands, atypical (*vs* typical) instances of the emotions would show heightened activity in the SN during valence focus.

METHODS

Participants

Sixteen right-handed, native English speakers from the Emory community, ranging in age from 19–30 years (eight female), participated in the study. Participants had no history of psychiatric illness and were not taking psychotropic medication. Each participant received \$100 in compensation.

Design

The fMRI experiment included two trial types that were critical for separating neural activity during scenario immersion from neural activity during valence focus. In 72 *complete* trials, participants immersed themselves in a fear, happiness or sadness scenario (i.e. scenario immersion), and then focused on and rated the valence quality of the feeling (i.e. valence focus). Equal numbers of typical and atypical scenarios were presented during the 24 complete trials for each category. In 18 *partial* trials, participants only immersed in a fear, happiness or sadness scenario (i.e. scenario immersion only), with equal numbers of typical and atypical scenarios making up the six trials per category. Partial trials were included so that scenario immersion events could be mathematically separated from subsequent focus events when complete trials were analyzed (Ollinger *et al.*, 2001a, 2001b). As necessary for this type of catch trial design, partial trials were unpredictable and accounted for 20% of all trials. The scenario immersion and valence focus conditions resulting from the 3 (category: fear, sadness, happiness) \times 2 (typicality: typical, atypical) design were later entered into atypical (pleasant fear, pleasant sadness, unpleasant happiness) *vs* typical (unpleasant fear, unpleasant sadness, pleasant happiness) statistical contrasts.

¹A catch trial design allowed for separation of neural activity during the two trial phases (see the ‘Methods’ section).

Table 1 Example scenarios used to induce atypical and typical experiences of fear, sadness and happiness.**Atypical scenarios**

You are jogging onto the soccer field, your cleats digging into the firm ground. You hear a booming voice welcome the crowd to the state championship. You jump in place to shake off the restlessness in your stomach. Looking around at your team, a rushing excitement deepens your competitive fire. You feel an energizing fear.

You are standing on your college quad, dressed in a smart looking cap and gown. You listen for the graduation decree and upon hearing it fling your cap upwards. Following energetic classmates, you sweat lightly as you march away a graduate. You catch a friend's eye and flashback to your delightfully lively freshman dorm. You feel a spirited sadness.

You are standing outside on break, conversing with a close coworker. You pause while your friend bravely describes shameful rumors circulating about you. You sense your stomach churning as you avert your watering eyes for a second. Still absorbing the stinging gossip, you are grateful for your friend's presence. You feel an agitated happiness.

Typical scenarios

You are walking to your car alone, the city parking deck dimly lit. You hear an explosive bang and see a man running with a pointed gun. You quickly drop behind a car and attempt to control your shallow breathing. You try to dismiss the horrendous vision of what will happen if he finds you. You feel a perilous fear.

You are walking into a friend's house, dropping by to return a movie. You witness your significant other in an intimate embrace with your friend. Your stomach is nauseated, the shocking infidelity settling into your body. Your mind is spinning trying to understand the terrible betrayal of trust. You feel a devastating sadness.

You are performing a challenging piano solo, your fingers working the keys. You finish the piece and receive thunderous applause as you rise. You bend at the waist into a deep bow and sense your heart thumping rapidly. Glowing with satisfaction, you continue to feed off the crowd's energy. You feel a proud happiness.

Italics indicate the core version presented in the scanner.

Notes. Scenarios also systematically varied in arousal (see Wilson-Mendenhall *et al.*, 2013). For comparison purposes, all the examples shown here are higher in arousal.

Six imaging runs consisted of one valence block and one arousal block, with block order counterbalanced across runs and with trials as events within blocks. Across the six runs in the experiment, each fear, sadness and happiness scenario was presented twice, once in an arousal block and once in a valence block (see Wilson-Mendenhall *et al.* (2013) for counterbalancing details of the four versions to which participants were randomly assigned). Arousal blocks were analyzed elsewhere (Wilson-Mendenhall *et al.*, 2013) and will only be mentioned when critical for describing the experiment. Within each valence block, four complete trials and one partial trial for each category were presented amidst jittered no-sound baseline periods (ranging from 3 to 15 s in increments of 3 s; average ISI = 6.3 s) in a pseudo-random order optimized by optseq2 software (Greve, 2002).

Materials

Scenarios written and recorded by the experimenters were designed to induce fear, sadness and happiness experiences. A full and core form of each scenario was developed, the core being a subset of the full form (Table 1). The full form provided a richly detailed and affectively compelling description of a fear, sadness, or happiness episode. The core form served to minimize presentation time in the scanner so that the number of trials necessary for a sufficiently powerful design could be implemented. In both forms, scenarios were explicitly categorized as fear, sadness or happiness to avoid ambiguity. The scenarios were designed to evoke typical valence in half of the scenarios (unpleasant fear and sadness; pleasant happiness) and to evoke atypical valence (pleasant fear and sadness; unpleasant happiness) in the other half. More details on the construction and selection of scenarios, as well as their arousal properties (which varied independently of valence), can be found in Wilson-Mendenhall *et al.* (2013).

To measure typicality of the scenarios in each emotion category, an independent sample of 28 participants ranging in age from 18 to 55 years (11 male; mean age = 30) rated the scenarios used in the neuroimaging design. Participants listened to the full versions of the scenarios and rated them on a scale from 1 (*poor example*) to 7 (*excellent example*) (see the supplementary materials for details). Using standard procedures for collecting typicality ratings, participants were asked to judge how good of an example each scenario was of its emotion category (fear, happiness, or sadness) (e.g. Barsalou, 1985). Scenarios were presented in the same order as during the neuroimaging study, with participants randomly assigned to one of the four versions.

Procedure

The experiment contained two training sessions and an fMRI scan session. The first training session occurred 24–48 h before the second training session, which was followed immediately by the scan session. During the two training sessions, participants actively practiced (i) vividly imagining the full versions of the scenarios they would hear later in the scanner, (ii) reinstating the rich imagery of each full scenario upon hearing the core version, and (iii) focusing on and rating the valence or arousal quality of the feeling state evoked by a scenario. Familiarity and immersion ratings collected during the training sessions suggest that participants easily generated emotions upon immersing themselves in the compelling real-world scenarios, atypical as well as typical (Supplementary Figure S1). Further detail on the training sessions can be found in the supplementary materials and in Wilson-Mendenhall *et al.* (2013).

Just prior to scanning, participants practiced several short runs of the task that they would perform in the scanner. During complete trials, participants were instructed to immerse themselves fully as they listened with eyes closed to the core version of a scenario lasting no longer than 8 s. A 1 s 'beep, beep, beep' that followed indicated that immersion in the emotional experience should continue as the participant centered in on the valence of the feeling, maintaining focus for 3 s. A 1 s cowbell then cued participants to rate their introspective sense of valence within the next 2 s, using the 5-point valence scale they had practiced earlier (very unpleasant, somewhat unpleasant, neutral, somewhat pleasant, very pleasant). During 9 s partial trials, participants heard a 1 s 'whoosh' sound when the 8 s scenario concluded, which signified the end of the trial. During baseline rest trials, participants did not perform a task, resting during the 3–15 s period of no sound.

Imaging and analysis

Images were acquired at the Emory Biomedical Imaging Technology Center on a 3T Siemens Trio scanner and preprocessed using standard methods in AFNI (Cox, 1996) (see the supplementary materials for details). Our analysis approach provided a comprehensive test of our hypotheses: (i) examine the atypical > typical contrast across categories based on the designed valence split, (ii) examine whether using the typicality ratings as the independent variable across categories yielded similar results to #1, and (iii) examine whether each emotion category showed the network results in #2 and/or #1 when modeled independently.

Valence-split analysis

At the individual level, trial onset times were specified to model the hemodynamic response using gamma variate functions convolved with event durations. Onsets of the pleasant and the unpleasant scenario events for each category were specified as separate scenario immersion conditions (i.e. an unpleasant and a pleasant condition for fear, sadness, and happiness; six conditions total). Likewise, the onsets of the pleasant and unpleasant focus events for each category were specified as separate valence focus conditions (six conditions total).² Scenario events included the 9 s during which participants heard the scenario (8 s) and subsequent auditory cue (1 s), with each scenario immersion condition made up of scenario events from the complete and the partial trials (Ollinger et al., 2001a, 2001b). Focus events included the 6 s during which participants focused on and rated the valence of the induced emotion. The betas resulting from each individual's regression analysis were then entered into a second-level random effects analysis. Group-level contrasts were computed for scenario immersion and for valence focus in which the atypical conditions (+1 pleasant fear, +1 pleasant sadness, +1 unpleasant happiness) were compared with the typical conditions (−1 unpleasant fear, −1 unpleasant sadness, −1 pleasant happiness) using voxel-wise, dependent sample *t*-tests.

Typicality rating amplitude modulation analyses

Because the typicality ratings for two of the three emotion categories clearly showed continuous, not discrete, properties (see Supplementary Figure S2), which are consistent with typicality *gradients*, we also conducted amplitude modulation or 'parametric' analyses. Two individual-level regressions were performed using the typicality ratings from the independent sample. Mean typicality was computed for each scenario (i.e. each item) using the behavioral data from the independent sample. In the first analysis, which examined the correlation between brain activity and the typicality ratings across categories, the onset times for all scenario immersion and valence focus events during valence blocks were specified, as were the trial-by-trial typicality rating data. The typicality data were mean centered and entered into the regression analysis as auxiliary behavioral covariates associated with scenario immersion events and with valence focus events. This procedure creates additional regressors in the model that scale the predicted BOLD response for each event by the typicality rating data. The resulting regression coefficients reflect the correlation between brain activity and the typicality rating data during scenario immersion and during valence focus.

The second analysis examined the correlation between brain activity and the typicality data within each emotion category. The critical difference between the first analysis and the second analysis was that the scenario immersion and valence focus conditions were each split into three conditions for the emotion categories fear, happiness, and sadness.

At the group level, each individual's voxel-wise beta map indicating the correlation between brain activity and the typicality rating data was entered into a one-sample *t*-test. In the first analysis, *t*-tests were computed on the beta maps for scenario immersion and for valence focus. In the second analysis, *t*-tests were computed on the beta maps for fear, happiness, and sadness during scenario immersion and on the beta maps for fear, happiness, and sadness during valence focus. In each case, the *t*-test was used to determine whether the voxel-wise means across individuals' beta maps were significantly different from zero.

² Arousal blocks were modeled analogously in the individual-level analyses, but were not examined at the group level, because our hypotheses targeted the valence blocks. The cues beginning each valence and arousal block were also modeled in the individual-level analysis.

Table 2 Typicality rating descriptive statistics presented by emotion category and by atypical/typical valence split (from the neuroimaging design)

Emotion category	Atypical		Typical	
	<i>M</i>	SEM	<i>M</i>	SEM
Fear	3.90	0.20	5.47	0.11
Happiness	2.90	0.23	6.26	0.12
Sadness	3.44	0.24	5.38	0.13

SEM is standard error of the mean computed across subject condition means.

Masking and thresholding

DMN and SN masks were obtained from a large-scale resting state study (Yeo et al., 2011). For the analyses across categories, a voxel-wise threshold of $P < 0.005$ was used with an extent threshold determined by AFNI ClustSim to produce a corrected threshold of $P < 0.05$ (DMN: 22 voxels, SN: 16 voxels, whole brain: 37 voxels). For the within-category analysis, a voxel-wise threshold of $P < 0.05$ was used with the $P < 0.05$ corrected extent threshold determined for each mask region in which significant clusters emerged in the across-category analyses (see Tables 4 and 6 for extent thresholds).

RESULTS

Typicality ratings

A 3 (emotion category) \times 2 (atypical/typical valence split) repeated measures ANOVA run on the typicality ratings from the independent sample revealed a main effect of typicality, $F(1,27) = 119.5$, $P < 0.05$. The scenarios we defined as typical instances using valence were rated significantly more typical than the scenarios we defined as atypical instances for each category (Table 2). To further assess the variance in the typicality ratings that was explained by valence, we computed the correlation between the valence item means from the imaging sample (i.e. the ratings made by participants during valence focus) and the typicality item means from the independent sample. For each emotion category, valence (where low–high values reflect the unpleasant–pleasant continuum) and typicality (where low–high values reflect the atypical–typical continuum) were strongly correlated.³ For fear and sadness, as scenario instances became more unpleasant, typicality increased; $r(22) = -0.60$, $P < 0.05$ and $r(22) = -0.83$, $P < 0.05$, respectively. For happiness, as scenario instances became more pleasant, typicality increased; $r(22) = 0.96$, $P < 0.05$.

Scenario immersion

During scenario immersion, we predicted that heightened activity in the DMN would be observed for atypical (*vs* typical) instances due to the increased conceptual processing required to situate the atypical instances. The DMN mask included 11 cortical clusters: (1) medial prefrontal cortex, (2) posterior cingulate/precuneus, (3/4) bilateral superior temporal sulcus (STS)/temporoparietal junction (TPJ), (5/6) bilateral temporal poles/anterior-to-mid STS, (7/8) bilateral inferior frontal gyrus (IFG), (9) left middle frontal gyrus (MFG), and (10/11) bilateral parahippocampal cortex.

Atypical > typical contrast across categories

As predicted and as Figure 1 illustrates, we observed reliably greater activity in the DMN during immersion in scenarios inducing atypical fear, sadness and happiness experiences than during immersion in

³ No other behavioral measure correlated significantly with typicality in all three categories.

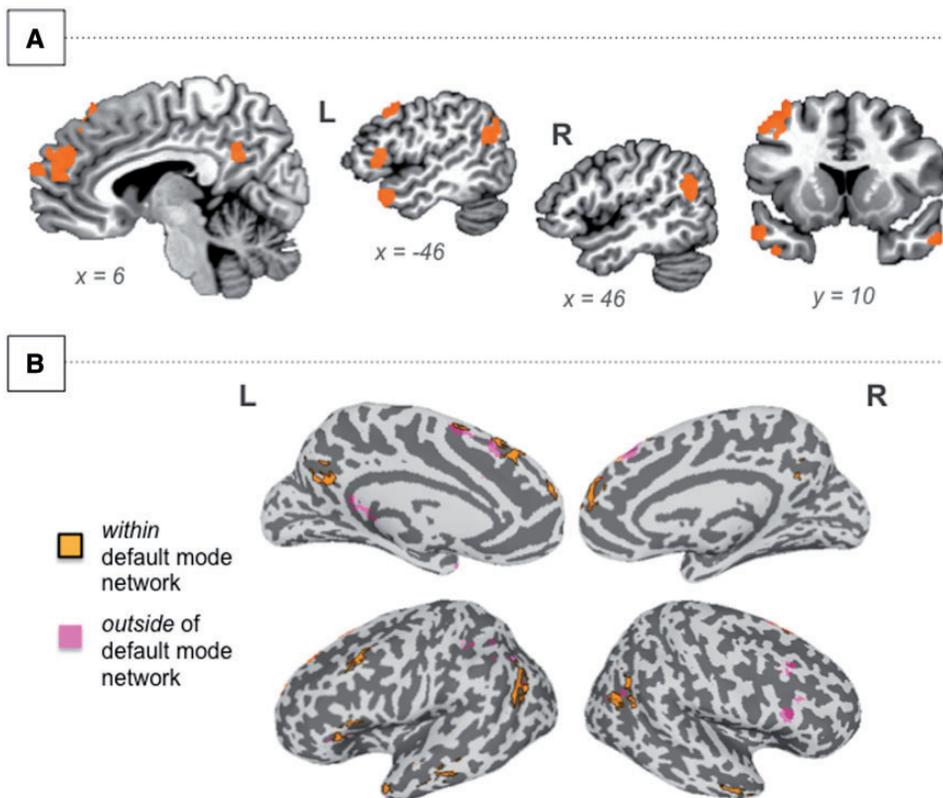


Fig. 1 (A) The DMN regions that emerged in the scenario immersion atypical > typical contrast across categories. (B) The overlap between the atypical > typical whole-brain pattern and the DMN. The inflated surface is only used for display purposes; analyses were not computed in this space.

Table 3 DMN regions that emerged in the scenario immersion analyses across categories

Brain region	Atypical > typical contrast				Typicality rating correlation					
	Spatial extent	Center		Mean	Spatial extent	Center		Mean		
	x	y	z	t	x	y	z	t		
dmPFC/SMA	117	-3	30	49	3.93	23	1	35	46	3.78
R Post STS/TPJ	100	49	-60	25	4.30	56	49	-59	24	3.95
dmPFC	98	0	53	24	4.01	48	-2	48	27	4.06
L MFG	68	-42	12	47	4.00	28	-44	11	47	3.75
L Post STS/TPJ	64	-42	-59	25	4.03	41	-43	-58	22	3.88
R Temp Pole/Ant STS	40	57	2	-18	3.77	36	53	8	-23	3.77
Post Cing/precuneus	40	-3	-54	29	3.60					
L IFG	38	-49	20	11	3.88					
L Temp Pole	34	-46	15	-21	3.99	57	-49	11	-23	4.04
L Ant STS	31	-60	-12	-9	3.53	68	-58	-9	-8	3.87

Notes. Spatial extent is the number of 27 mm³ functional voxels. L is left and R is right. Ant is anterior and Post is posterior. dmPFC is dorsomedial prefrontal cortex and SMA is supplementary motor area. STS is superior temporal sulcus and TPJ is temporoparietal junction.

scenarios inducing typical experiences of the same emotions (and no regions displayed the opposite pattern—more activity during typical instances). Of the 11 regions defining the DMN, 8 were significantly more active during atypical instances (Figure 1A). In addition to the core midline medial prefrontal cortex and posterior cingulate hubs, heightened activity was observed in bilateral temporal poles/anterior STS, bilateral posterior STS/TPJ, left IFG, and left MFG (Figure 1A and Table 3). The whole-brain contrast revealed very little activity outside of the DMN, with additional clusters located primarily in right

lateralized frontal regions (Figure 1B and Supplementary Table S1). Furthermore, consistent with the idea that this network is generally involved in the scenario immersion process, the typical instances showed activity significantly above baseline in many DMN regions (but significantly less activity than atypical instances) (see Supplementary Figure S3 and related text).

Typicality rating analysis across categories

Figure 2A illustrates that activity in regions throughout the DMN increased as scenario instances became less typical (more atypical). We observed this pattern in 6/8 of the DMN regions identified in the atypical > typical valence-split analysis, including medial prefrontal cortex, bilateral temporal poles/anterior STS, bilateral posterior STS/TPJ, and left MFG (Figure 2B and Table 3). The only region emerging in this analysis that was outside of the DMN was a cluster in the right inferior parietal lobe (Supplementary Table S2).

Typicality rating analysis within each category

If the robust DMN activity observed when analyses were conducted across categories is due to domain-general mechanisms that produce many different emotional experiences, activity in the DMN should not be driven by a single emotion category. As shown in Table 4, distributed activity throughout the DMN was observed when the correlation between the typicality rating data and brain activity was assessed within each emotion category (the size of the circle in Table 4 represents the relative size of the cluster in the region specified). With the exception of left lateral prefrontal cortex, significant correlations were observed in two or more categories for every region of the DMN. This pattern of results also demonstrates that the pattern of DMN activity that

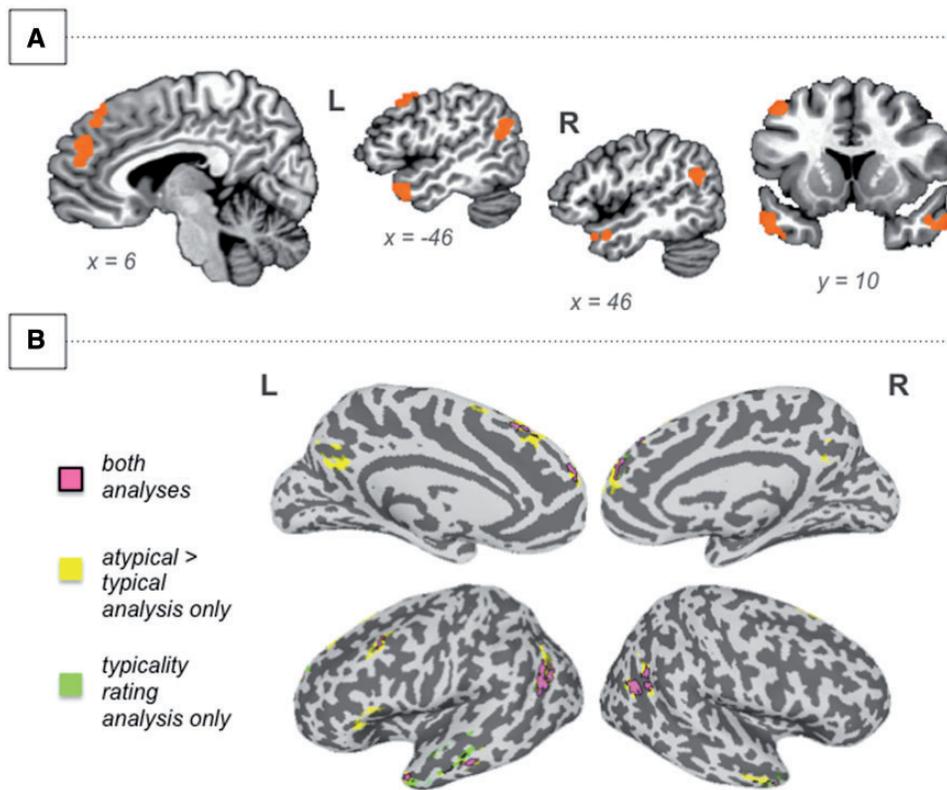


Fig. 2 (A) The DMN regions in which brain activity correlated with the typicality rating data across categories. (B) The overlap between the typicality rating analysis and the atypical > typical analysis shown in Figure 1. The inflated surface is only used for display purposes; analyses were not computed in this space.

Table 4 For each emotion category, clusters in the DMN that showed a significant correlation with the typicality ratings

Default mode network	Fear	Happiness	Sadness
Medial prefrontal cortex	○ ○ ○	●	○
Posterior cingulate/precuneus	●	●	
L temporal pole/anterior STS	●	●	
L posterior STS/TPJ	●	●	
R temporal pole/anterior STS	●	●	
R posterior STS/TPJ	●	●	●
L inferior/middle frontal gyrus		●	
R inferior frontal gyrus		●	●

The size of the circle represents the size of the cluster.
 Notes. The four sizes of circles shown here represent extents of 30–60 voxels, 60–90 voxels, 90–120 voxels and >120 voxels. Region-specific corrected cluster extent thresholds: 101 (medial prefrontal cortex), 81 (posterior cingulate), 53 (temporal pole/anterior STS), 55 (posterior STS/TPJ), 57 (left inferior/middle frontal), and 36 (right inferior frontal). A white circle indicates a cluster that did not pass the corrected threshold, but that was greater than 30 contiguous voxels (note that for fear, the sum of the three medial prefrontal clusters is greater than the corrected threshold). A black border indicates a large cluster that spanned multiple regions.

emerged in the analyses across categories was not skewed by a robust valence effect in one category.

Valence focus

During valence focus, we predicted that heightened activity in the SN would be observed for atypical (*vs* typical) instances due to the increased demands on integrating fluctuating body signals with sensory and social context to report a subjective feeling. Although the regions included in this network sometimes vary, it is clear that core nodes exist in anterior cingulate and in bilateral fronto-insular cortex (Seeley et al., 2007; Cauda et al., 2011; Yeo et al., 2011; Lee et al., 2012; Touroutoglou et al., 2012). The SN (Seeley et al., 2007) is also referred to as the ventral attention network in the attention literature (Corbetta et al., 2008). The SN mask that we used included a number of additional regions that have been implicated in ‘reorienting’ to the external environment: bilateral premotor cortex, mid cingulate, bilateral MFG, and bilateral middle temporal gyrus. Because internally oriented assessment of one’s affective state (*vs* externally oriented visual search) is likely to involve integrating shifting body signals with other forms of information, our hypotheses specifically targeted the fronto-insular and anterior cingulate regions of the SN.

Atypical > typical contrast across categories

As predicted, we observed reliably greater activity in the SN during valence focus for atypical emotional experiences (relative to typical emotional experiences). As Figure 3A and Table 5 illustrate, both the anterior cingulate and fronto-insular hubs of the SN showed this pattern of activity. Because activity during valence focus for typical instances was clearly above baseline (Supplementary Figure S4), neural activity in these regions appears to reflect general processing involved

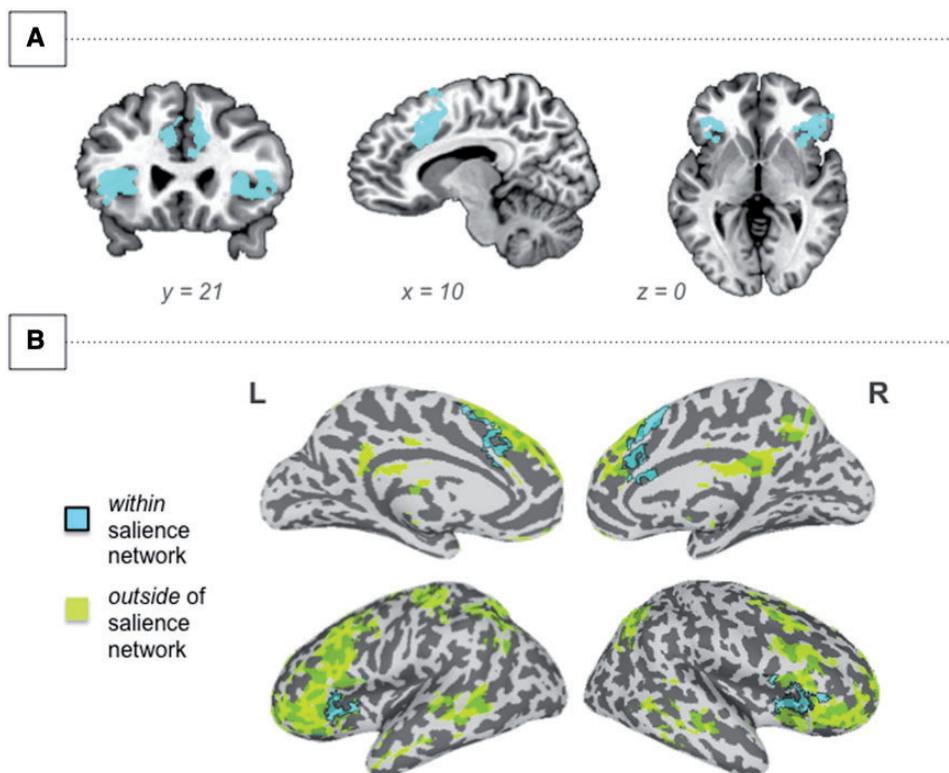


Fig. 3 (A) The SN regions that emerged in the valence focus atypical > typical contrast across categories. (B) The overlap between the atypical > typical whole-brain pattern and the SN. The inflated surface is only used for display purposes; analyses were not computed in this space.

Table 5 SN regions that emerged in the valence focus analyses across categories

Brain region	Atypical > typical contrast					Typicality rating correlation				
	Spatial extent	Center			Mean	Spatial extent	Center			Mean
		x	y	z			t	x	y	
Ant Cing/SMA	234	4	14	44	4.83	143	4	14	43	4.11
L Fronto-insular	109	-35	23	5	5.29	94	-35	23	5	4.87
R Fronto-insular*	142	40	24	4	4.23					
(R Ant Insula)						36	32	23	4	4.24
(R IFG/OFC)						27	45	25	3	3.83

Notes. Spatial extent is the number of 27 mm³ functional voxels. L is left and R is right. Ant Cing is anterior cingulate and SMA is supplementary motor cortex. IFG is inferior frontal gyrus and OFC is orbitofrontal cortex. *R Fronto-insular cortex is broken down into R Ant Insula and R IFG/OFC, signified by the indentation and parentheses, because two distinction clusters were observed in right fronto-insular cortex in the typicality rating analysis.

in focusing on and reporting an internal feeling state, which was heightened during the atypical instances. No significant clusters emerged in the premotor, cingulate, middle frontal, or middle temporal regions of the SN.

As shown in Figure 3B, the whole-brain analysis also revealed reliably greater activity in fronto-parietal attention networks (Seeley et al., 2007; Posner, 2012) when participants focused on the valence evoked by atypical emotional experiences (see also Supplementary Table S3 and related text). Dorsal anterior insula and anterior cingulate are highly connected with fronto-parietal attention networks, interacting with these regions to guide top-down attention and cognitive control (Touroutoglou et al., 2012). Consistent with the increased activation in attention networks, we observed significant effects when we examined

the relationship between reaction time and typicality during valence focus. As instances of an emotion category became more atypical, reaction time tended to increase (see Supplementary Table S4 and related text).

Typicality rating analysis across categories

Figure 4A illustrates that activity in anterior cingulate and bilateral fronto-insular cortex increased as scenario instances became less typical (more atypical) (see also Table 5). Figure 4B displays the large degree of overlap with the valence-split atypical > typical contrast. The whole-brain pattern was also similar to the pattern described above, with extensive activity in fronto-parietal attention networks (Supplementary Table S5).

Typicality rating analysis within categories

As shown in Table 6, activity in anterior cingulate and fronto-insular cortex was observed in each emotion category when the correlation between the typicality rating data and brain activity was assessed within the emotion categories (the size of the circle in Table 6 represents the relative size of the cluster in the region specified). These results suggest that the typicality effect is independent of valence (occurring during both atypical pleasant and atypical unpleasant instances) and that these regions support domain-general processing that occurred during valence focus in all three categories.

DISCUSSION

Consistent with a psychological construction approach to emotion (Barrett, 2012, 2013), domain-general neural systems were implicated across three categories of emotional experience, displaying increased neural activity during more atypical instances (vs typical instances).

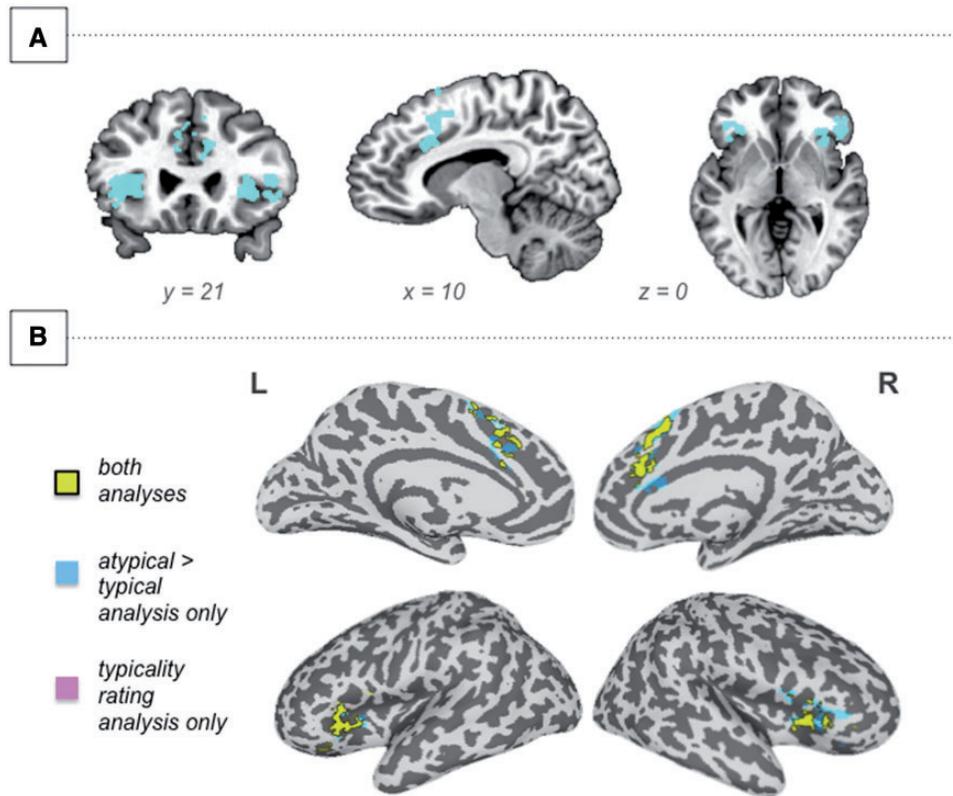


Fig. 4 (A) The SN regions in which brain activity correlated with the typicality rating data across categories. (B) The overlap between the typicality rating analysis and the atypical > typical analysis shown in Figure 3. The inflated surface is only used for display purposes; analyses were not computed in this space.

Table 6 For each emotion category, clusters in anterior cingulate and fronto-insular regions of the SN that showed a significant correlation with the typicality ratings

Saliency network	Fear	Happiness	Sadness
Anterior cingulate/SMA	●	●●	●
R Fronto-insular		●	●
L Fronto-insular	●	●●	●

The size of the circle represents the size of the cluster. Notes. The three sizes of circles shown here represent extents of 60–90 voxels, 90–120 voxels and >120 voxels. Region-specific corrected cluster extent thresholds: 64 (anterior cingulate/SMA) and 54 (fronto-insular).

In the same way that slower learning rates and increased RTs indicate decreased processing efficiency for atypical category instances, our results analogously suggest that decreased processing efficiency occurs within coordinated brain networks for atypical category instances.

Across many different kinds of categories, typicality is a dimension that indexes important differences in processing (see Jenkins and Mitchell (2010) for a similar point about ambiguity). Identifying the ‘core’ network operations that underlie the differences in processing observed here will require further empirical work, but the existing literature suggests that these operations are not tightly tied to specific content domains (e.g. emotions, beliefs, or attitudes) (Laird et al.,

2011; Lindquist and Barrett, 2012; Barrett and Satpute, 2013). We propose that immersing in imagined socio-emotional situations (i.e. scenario immersion) or experiencing similar situations in the real world involves situated, integrative conceptual processing supported by the DMN (Wilson-Mendenhall et al., 2011; Barrett, 2012), and that this processing is less efficient when situating an atypical instance of an emotion category. We further propose that focusing on and reporting one’s affective state (i.e. valence focus) involve integrating fluctuating body signals with the sensory and social context of an emotional situation (Menon and Uddin, 2010; Barrett and Satpute, 2013), processing that is supported by the SN and that is less efficient when an affective feeling is not as easily categorized.

Less efficient processing of atypical instances has important implications for learning, memory, and categorization. Atypical instances of a category are generally learned more slowly, are less available during recall, and are more difficult to categorize (Smith et al., 1974; McCloskey and Glucksberg, 1979; Casey, 1992; Larochelle and Pineau, 1994; Russell and Fehr, 1994). Learning to categorize atypical ‘fuzzy’ instances of emotions and to differentiate between instances within an emotion category is important for mental health because it supports identifying and changing dysfunctional patterns of behavior (e.g. Beck and Dozois, 2011; Masley et al., 2012). It may also help resolve anxiety and stress (Lindquist and Barrett, 2008; Demiralp et al., 2012).

A single word (e.g. fear, happiness, or sadness) is often used to refer to the many different instances of an emotion category, which may explain why it is routinely assumed that within-category variability either does not exist or that it is unimportant (in contrast, the different instances of concrete categories often have specific words that name them). Our findings suggest that affective valence plays an important role in determining typicality gradients, but we are likely

underestimating the contributions of other affective, social, or situational properties that we did not measure or manipulate in this study. Furthermore, typicality gradients are not static—they dynamically change with context (Barsalou, 1987) and they are often shaped by goal-derived ideals as opposed to a stable prototypical average (Barsalou, 1985).

It is becoming increasingly clear that to understand human emotional experiences, it is essential to study the tremendous variability that exists *within* common emotion categories such as fear, happiness, or sadness. This was the essence of William James' charge to psychology over a century ago.

SUPPLEMENTARY DATA

Supplementary data are available at SCAN online.

CONFLICT OF INTEREST

None declared.

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