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Opinion

The Default Mode Network's Role in Discrete Emotion

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Emotions are often assumed to manifest in subcortical limbic and brainstem structures. While these areas are clearly important for representing affect (e.g., valence and arousal), we propose that the default mode network (DMN) is additionally important for constructing discrete emotional experiences (of anger, fear, disgust, etc.). Findings from neuroimaging studies, invasive electrical stimulation studies, and lesion studies support this proposal. Importantly, our framework builds on a constructionist theory of emotion to explain how instances involving diverse physiological and behavioral patterns can be conceptualized as belonging to the same emotion category. We argue that this ability requires abstraction (from concrete features to broad mental categories), which the DMN is well positioned to support, and we make novel predictions from our proposed framework.

Network Models of Emotion

Neuroscience has learned a lot about the **representation of emotion** (see Glossary) and its neural mechanisms over the past few decades. Traditionally, it was assumed that each **discrete emotion** such as fear, anger, sadness, and joy emerged from a specific anatomically defined region or circuit traversing the limbic system and brainstem nuclei [e.g., a hypothalamic–amygdala–periaqueductal gray (PAG) circuit] [1–3]. These models have given way to a newer, functional network approach in which it is proposed that the processes constituting emotions are widely distributed across several large-scale functional networks of the brain [4–8].

Guided by this approach, much research in **affective** neuroscience has focused on the so-called salience network [9] since it includes many of the aforementioned limbic areas including the hypothalamus, amygdala, and cortical areas that process visceral information (e.g., the insula and cingulate cortex) [10–12]. Yet, the salience network does not operate in isolation when creating emotion. Rather, discrete emotions appear to emerge through dynamic interactions between multiple functional networks [6,13]. These findings dovetail with a handful of recent multivariate pattern analysis studies of emotion [7,14,15] showing that the patterns of functional activation related to discrete emotional experiences also do not reside in a single network but instead are widely distributed across multiple, large-scale functional networks (Box 1).

Importantly, we [4,5] and others [6,16] have proposed that networks are not unique to emotion, but contribute to the variety of subjective categories for mental phenomena that we refer to (in Western culture) as emotions, thoughts, memories, etc. That is, there is a domain-general mapping of functional networks with mental state categories. What remains unclear is what role each network plays when creating these mental states. In this paper, we specifically focus on the role of the default mode network (DMN) in emotion. Like the salience network and other large-scale functional networks, the DMN was discovered in recent human neuroimaging studies [17,18] and connectomics [19,20]. However, unlike nodes of the salience network, the DMN has

Highlights

Emotions involve the coordinated activity of large-scale functional networks. The DMN has been linked with emotion but its mechanistic role remains unclear.

Most prior accounts link DMN to emotion given the role of ventromedial prefrontal cortex (VMPFC) in more general affective processing (valence and arousal) or the broader DMN in generating internal states.

Data from human neuroimaging, electrical stimulation, and lesion studies suggest that the DMN is implicated in representing discrete experiences of emotion (fear, anger, sadness etc.).

The DMN also involves the usage of prior experience and knowledge to guide information processing to support abstraction and granularity.

A theoretical framework is presented for how emotions involve representations at multiple levels of abstraction, and also how representations of discrete emotions vary in terms of their granularity.

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not had the same trajectory of being as directly associated with emotion. As outlined in Table 1, the DMN has largely been associated with emotion to the extent that the DMN contains nodes (e.g., ventromedial prefrontal cortex; VMPFC) associated with affect (i.e., representation of pleasant and unpleasant states; somatovisceral activation) or insofar as it is believed to serve other functions that may relate with emotions (e.g., generating internal vs external states). Indeed, many DMN nodes have only recently been affiliated with discrete emotions, and largely on the basis of neuroimaging meta-analyses that show reliable increases in activation within DMN nodes during experiences of emotion [21,22].

Given the multiple functional roles attributed to the DMN (for a review, see [18]), there is little consensus as to what the DMN is doing during emotion. It is unclear whether the DMN plays a direct and constitutive role in creating discrete emotions beyond the role of the VMPFC in generating affect, or whether the DMN instantiates modulatory processes that are indirectly related with emotional experience (Table 1). Here, we propose that the DMN is actually playing a constitutive function in creating instances of discrete emotions (e.g., anger, disgust, fear, etc.): DMN nodes facilitate the ability to experience concrete physiological sensations and situated behaviors as instances of more abstract emotion categories. This ability has been previously referred to as **conceptualization** and meaning making [23–25] at the psychological level of analysis. Here, we develop this approach further to more concretely describe the process of conceptualization (Box 1), its relationship with levels of **abstraction** and **granularity** (Box 2), and the role of the DMN in discrete emotions.

We first summarize findings on the neuroscience of emotion that implicate the DMN in creating discrete emotional experiences. We then integrate a diverse body of research to propose that the

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Box 1. Theory of Constructed Emotion

According to the **Theory of Constructed Emotion**, discrete emotions are not mechanisms that each have their own unique biological underpinnings, but instead are collections of mental representations that are created from domain general processes in the brain and body [4,21,120]. Using fear as an example, people feel fear in many different situations including situations involving spiders [121], heights [122], social evaluation [123], etc. Each situation may involve different physiological [124], behavioral [125], and neural [21,126] patterns. It is the collection of these potentially diverse patterns that makes up the category fear. There is currently no known neurobiological essence for fear (e.g., a singular neural circuit) that is shared across all instances and individuals [89,120,127]. It has been suggested that neural circuits for adaptive behaviors (e.g., freezing) may comprise such a neurobiological essence, but this view cannot accommodate the many instances of fear in which freezing does not occur. The constructionist theory proposes that a person experiences fear when they experience a set of highly situated physiological, behavioral, contextual features that conform to that person's unique abstract category for fear. This ability is known as conceptualization [128] and refers to the use of prior experience and semantic knowledge in processing sensory input from the internal body and external world via processes referred to as categorization, simulation, prediction, or pattern completion [63,120,126,128].

Figure I provides an illustration of the theoretical model. The table outlines four hypothetical instances of fear that involve a set of features that vary in kind (along rows) and intensity (number of +s). For example, Instance 1 may involve rock climbing (heights), being watched (social evaluation), and physiological and behavioral responses (hyperventilation and freezing). Instance 2 may involve encountering a tarantula while hiking, bradycardia, redistribution of blood to the legs, and eye widening to increase visual input. Instances can be represented in a high-dimensional feature space (simplified to two dimensions for the sake of illustration). Situated conceptualizations are modeled as a landscape of 'attractor basins'. Grouping together the full collection of variable instances as fear is, by definition, an abstract category that refers to the representational space of fear [25]. The abstract representation of those instances as all belonging to the same category of fear may differ between individuals (Box 2) and may be uniquely human.

In Figure I, the red dot depicts a future instance that becomes an instance of fear when it is conceptualized as such [23]; that is, when the features of that instance are organized and made meaningful with respect to category knowledge about fear and thus assimilated as an instance of the category. Its position in the high-dimensional space implies that it will be understood with respect to the cluster on its left (i.e., be grasped by the corresponding attractor basin). Conceptualizations impose meaning on future instances insofar as prior instances guide how the collection of features of the current instance are organized and made meaningful. This imposition of meaning is particularly evident when a given instance is warped to assimilate the available concepts, for example, in the category boundary effect (for reviews, see [84,129,130]).
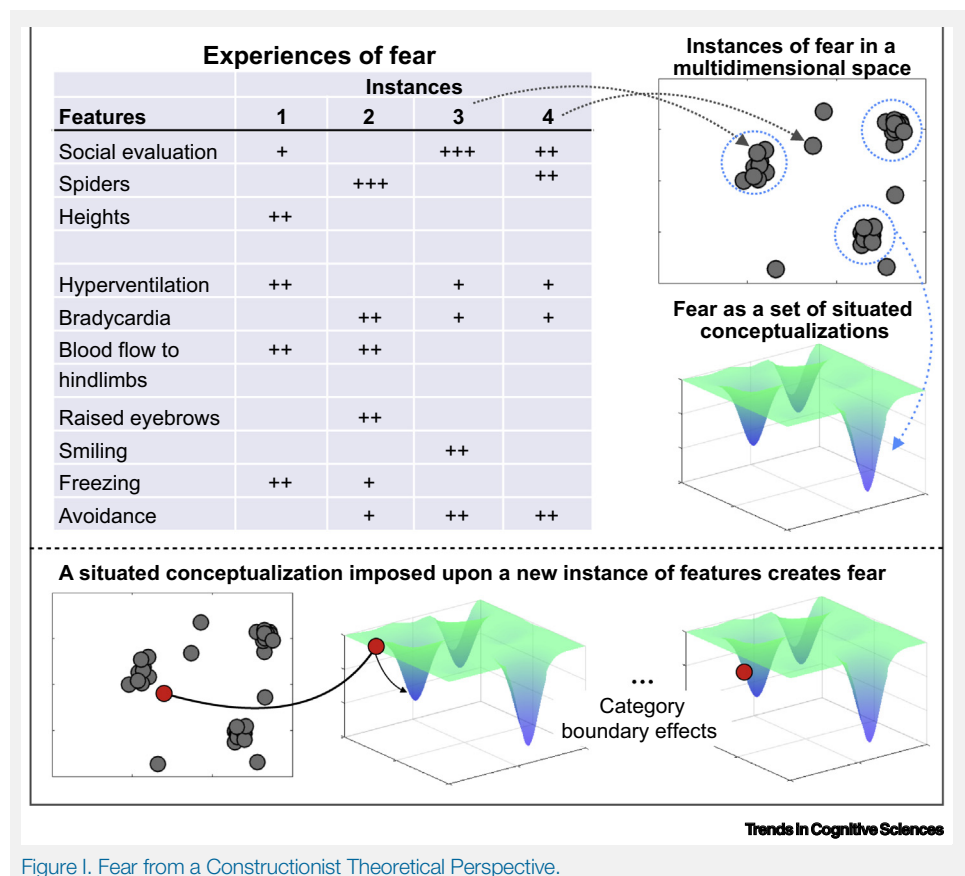

Glossary

Abstraction: process of generalization in which commonalities can be observed between two otherwise heterogeneous features, instances of multiple features, two or more situated conceptualizations, etc. For instance, a person can group together two instances as fear even if they have completely different situated properties (e.g., an instance of fear of heights and fear of public speaking may share little in common in terms of the physical contexts they occur in, the physiological state of the body, the thoughts a person is experiencing, the visual sensations being taken in, yet nonetheless are both experienced as instances of the same category).

Affective: term used to describe anything that is experienced as having the qualities of pleasantness or unpleasantness and high or low activation. This term pertains to emotions but is also used to describe attitudes, evaluations, and other cognitive phenomena that implicate valence and arousal.

Conceptualization: process of drawing on prior experiences and knowledge to make meaning of one's current sensations (from both outside and inside the body). Situated conceptualization refers to the fact that conceptualizations occur in context and thus draw on situation-specific knowledge. When drawing on conceptual knowledge about fear, a person accesses specific prior instances of fear such as experiencing fear in the context of a boss versus experiencing fear in the context of a spider.

Discrete emotion: experience of an affective state as a discrete and bounded event that can be labeled with emotion words such as anger, disgust, fear, etc. Discrete emotions may stand in contrast to more general experiences of affect as feelings of pleasure or displeasure and high versus low activation (e.g., some discrete instances of fear, anger, and disgust may share similar amounts of affective pleasure and activation).

Granularity: refers to the differentiation of a person's emotional experiences. A person with moderate granularity might feel fear in one context, sadness in another, and disgust in another; a person high in granularity might further differentiate between fear vs anxiety, anger vs frustration, and also have more nuanced conceptual knowledge about

Figure I. Fear from a Constructionist Theoretical Perspective.

The figure contains the following labeled tables and panels:

Experiences of fear

Features	Instances 1	2	3	4
Social evaluation	+		+++	++
Spiders		+++		++
Heights	++			
Hyperventilation	++		+	+
Bradycardia		++	+	+
Blood flow to hindlimbs	++	++		
Raised eyebrows		++		
Smiling			++	
Freezing	++	+		
Avoidance		+	++	++

Instances of fear in a multidimensional space

Fear as a set of situated conceptualizations

A situated conceptualization imposed upon a new instance of features creates fear

... Category boundary effects

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DMN has structural and functional features that suggest it is well suited to support conceptualization and abstraction. Our account leads to novel predictions regarding when the DMN is more or less in demand when creating emotional experiences, and how the function of the DMN in emotion varies depending on phylogenetic and ontogenetic trajectories and health versus disease.

The DMN

The DMN refers to a set of brain regions that show greater metabolic activity during rest in comparison with other brain regions [17], greater functional activity during rest than when engaged in a cognitive task [26], and greater temporal correlations in functional activity with each other than with other brain regions [19,20]. Researchers hypothesized that during rest, people are likely to engage in internally focused processes such as mind wandering [26–28]. It was thus thought that increased activation during rest may reflect mental processes such as thinking about the future or past or about the self or social situations – all of which are phenomena that may also incidentally evoke affect and emotion. Subsequent studies confirmed the involvement of the DMN in internally focused states (for a review, see [18]) such as prospective and autobiographical memory [29,30], rumination [31,32], social cognition [33,34], valuation [32,35], internal mentation [36], and conscious awareness [37].

Of the studies that have linked the DMN to emotion, many do so incidentally, insofar as emotions are thought to relate with phenomena already associated with the DMN (e.g., theory of mind [33] or internal mentation [35]). Studies have also linked the DMN to emotion because it encompasses

emotions. People low in granularity do not differentiate amongst their emotions across instances (e.g., discrete emotions like fear, sad, or disgust are not keenly separable experiences and converge into a one dimensional representation of feeling corresponding with displeasure). These individuals have a paucity of conceptual knowledge about emotion [98,131,134].

Representational content: information that distinguishes different states (e.g., discrete emotions) from one another. This information can be estimated from functional brain activity (e.g., patterns amongst voxels in the brain that help to differentiate one emotion from another).

Representation of emotion: this phrase is sometimes used to refer to how affect is represented; how emotion as a broad category (i.e., in comparison with social cognitions or thoughts) is represented; or how a discrete emotion such as anger is represented as a unique activation pattern for all instances of anger. We use this phrase to refer to the general notion that discrete emotions must, in some way, be represented. However, our usage is nonspecific about whether the representation for a given emotion category is invariant across instances versus involves heterogeneous spatiotemporal patterns; whether it is the same or varies across individuals; and whether it is conserved across species.

Theory of Constructed Emotion: a version of constructionist theories of emotion that hypothesizes that emotions are created via the combination of more basic psychological (and corresponding neural) phenomena that are not specific to emotion. The theory of constructed emotion focuses on the role of affective sensations and conceptualization in creating emotion.

Table 1. Proposed Functional Role of the DMN with Emotion

Neuroanatomical focus of DMN	Proposed function	Refs
VMPFC	Generating/representing emotional arousal	[110]
VMPFC/MPFC/ACC[a]	Representation of affect, integration of emotion, and cognition	[17]
VMPFC/MPFC/ACC	Internally-generated states (e.g., anticipatory anxiety)	[111]
VMPFC/DMPFC	Representation of affective states (i.e., as part of a multifaceted self), integration of emotion and cognition	[35]
VACC/OFC/MPFC/PCC	Representation of affect, integration of emotion, and cognition	[112]
Medial temporal lobe, precuneus, PCC, retrosplenial cortex, TPJ, lateral PFC, MPFC, lateral temporal lobe	Representation of emotional states as a result of engaging in autobiographical memories or as part of the computations involved in theory of mind (i.e., for others' emotions)	[33]
VACC/MPFC	Internally generated states (e.g., emotion or social contexts)	[113]
Medial temporal lobe, precuneus, PCC, retrosplenial cortex, TPJ, lateral PFC, MPFC, lateral temporal lobe	Internally-generated states (e.g., enhanced emotion dysregulation in depression)	[38]
Medial temporal lobe, precuneus, PCC, retrosplenial cortex, TPJ, lateral PFC, MPFC, lateral temporal lobe	Integration of cognitive and emotion processing	[114]
Orbitofrontal cortex, ACC, MPFC, lateral PFC, precuneus, superior temporal cortex, lateral temporal cortex	Representation of pleasant states	[115]
VMPFC, PCC, precuneus, amygdala	Regulation and processing of emotion	[116]
Anterior MPFC and PCC DMPFC, temporal pole, lateral temporal cortex, TPJ	Anterior MPFC and PCC hubs: valuation of personally significant/affective information DMPFC subsystem: representing mental states of self and other (including emotions)	[117]
VMPFC; amygdala, striatum and midbrain, insula and lateral prefrontal cortex; PCC and intraparietal sulcii.	Combining elemental units of information – from sensory systems, interoceptive cues, long-term memory – into a Gestalt representation of how an organism is situated in its environment, which then drives predictions about future events	[24]
ACC/DMPFC, PCC/precuneus (partially overlaps with a temporal–amygdala–orbitofrontal network and hippocampal–diencephalic and parahippocampal–retrosplenial network)	Introspective, self-directed thought (pain perception, self-knowledge, autobiographical memory, mentalizing, empathy); disorder in the network is associated with depression, anxiety, obsessive–compulsive disorder, attention deficit hyperactivity disorder	[76]
Medial prefrontal cortex (VMPFC vs DMPFC)	VMPFC: affect; processing approach- and avoidance-relevant stimuli. DMPFC: processing mental states and episodic memory.	[118]
Hippocampal formation, parahippocampal cortex, retrosplenial cortex, and posterior inferior parietal lobule; DMPFC, temporal pole, lateral temporal cortex, and TPJ	MTL sub-system: autobiographical retrieval DMPFC subsystem: mentalizing (representing mental states, including emotions, of self and others)	[36]
VMPFC, DMPFC	Internally generated states (e.g., emotion); self-judgments (e.g., valence of feelings)	[18]
VMPFC, DMPFC, PCC, anterior temporal lobe	Nodes separately process functions such as representation of affect, attention to internal affective states, affective working memory, and emotion concepts	[119]
Medial temporal lobe, precuneus, PCC, retrosplenial cortex, TPJ, lateral PFC, MPFC, lateral temporal lobe	Integrating sensory representations of the internal milieu with the rest of the brain	[77]

Table 1. (continued)

Neuroanatomical focus of DMN	Proposed function	Refs
Medial temporal lobe, precuneus, PCC, retrosplenial cortex, TPJ, lateral PFC, MPFC, lateral temporal lobe	Representing parts of concepts (including emotion concepts) by instantiating simulations and sending predictions that alter processing through the entire cortical sheet, terminating in primary sensory and motor regions.	[25]

[a]Abbreviations: ACC, anterior cingulate cortex; DMPFC, dorsomedial prefrontal cortex; PCC, posterior cingulate cortex; TPJ, temporoparietal junction; VACC, ventral ACC.

the VMPFC, which itself is known to be involved in generating affective states via modulation of autonomic and endocrine activity [10,38]. Indeed, individuals with lesions to this area show impairments in self-reported affective intensity [39], affect-based decision-making [40], understanding affective cues in others [41], perception of valence in facial expressions [42], and a host of other affect-related phenomena. The DMN, more broadly, is thus sometimes implicated in affective dysregulation [38,43].

Although all discrete emotions fundamentally involve sensations in the viscera that are experienced as valence and arousal (i.e., affect), it is unclear whether and how these functions contribute to the distinctness of discrete emotions. For example, anger, disgust, and fear are all typically considered to be high arousal, negative valence affective experiences [23,44,45], and so affect alone is unlikely to provide information that distinguishes between these emotions. Rather, accumulating findings from functional neuroimaging experiments [7,14,15,46], neuroimaging meta-analyses [21,22], and intracranial electrical stimulation [47] and lesion [48,49] studies, suggest that the DMN carries **representational content** that distinguishes between discrete emotions above and beyond affect.

DMN and Discrete Emotions: Neuroimaging Studies

Meta-analyses summarizing across hundreds of neuroimaging studies have consistently revealed a role for DMN regions; DMN regions showed greater than chance activation magnitudes during various discrete emotional experience [4,5,21,22,50]. While suggestive, the univariate analytical approaches these initial studies used were not ideal for testing which brain regions carried information for experiencing discrete emotions as specific and differentiable states. More recent information theoretic approaches [51] suggest that mental phenomena are represented in the pattern of activation across voxels spanning multiple brain regions. These studies use multivoxel pattern analysis (MVPA), which assumes that the neural basis for a given emotion category, such as anger, is informed not only by voxels that show increasing activity during anger, but also by voxels that show no change in activation and even those that show reduced activity during anger. Informative voxels may also be spread across the brain instead of in a contiguous cluster. Machine learning techniques are used to diagnose which discrete emotion category is most relevant given a pattern of activation. Consistent with our hypothesis that the DMN is important for representing discrete emotions, studies using MVPA suggest that the classification of discrete emotional experiences involves voxels spanning the DMN (and are widely spread throughout the known subnetworks of the DMN; see Figure S1 in the supplemental information online [36]). Figure 1 illustrates this pattern of findings in four studies that have used this approach [7,14,46,52], which themselves span a range of types (meta-analysis vs single study), induction methods (movies, imagery, audio clips, etc.), and analyses (generative vs discriminative algorithms). Overall, these results suggest that nodes spanning the DMN carry representational content for discrete emotions, a conclusion also supported by the brain stimulation and lesion literature.

DMN and Discrete Emotions: Brain Stimulation and Lesion Studies

A small body of brain stimulation and lesion studies suggests that changes in discrete emotional experiences occur when DMN nodes are causally manipulated or compromised. Dozens of intracranial stimulation studies conducted over the past several decades have tested whether stimulation of various brain regions triggers an emotional experience. While individual intracranial stimulation studies rarely target more than one region and often focus on subcortical structures, a recent comprehensive review of studies conducted since the 1950s showed that emotional experiences also occur when stimulating several cortical DMN nodes [47]. Of the 64 studies published since the 1950s, 39 found an effect of electrical stimulation on emotional experiences, and of those, ten showed that stimulation of cortical regions of the DMN produced an experience of emotion. For instance, stimulation of the temporal pole resulted in reports of anxiety and sadness in one study [53] and happiness in another [54]. Stimulation of the superior temporal gyrus (STG) elicited experiences of fear [55] and stimulation of the inferior frontal gyrus (IFG) elicited experiences of mirth [47,56]. As for lesion studies, in perhaps the most pertinent study addressing this question to date [57], 23 stroke patients with focal brain lesions completed separate questionnaires about their daily discrete emotional experiences (e.g., frequency of sadness). Using voxel-based symptom-lesion mapping to correlate neural damage with psychological outcomes, greater damage in the right anterior temporal lobe was associated with reduced experiences of discrete emotions in daily life. These findings converge with the intracranial electrical stimulation studies, and also the broader neuroimaging literature, in supporting the view that the DMN plays a constitutive role in creating discrete emotional experiences.

There is also a sizeable neuropsychological literature on emotion perception that provides converging support for the role of the DMN in discrete emotion, more generally. While emotion perception and experience are distinct mental phenomena, our constructionist model, and other simulationist accounts [58,59], proposes that these phenomena may nevertheless share the same domain-

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Box 2. Emotion Representation Varies in Abstraction and Granularity

Figure I (top) illustrates the nested hierarchy of increasing abstraction from broad and abstract categories of mental experience to concrete sensory and motor features that are associated with those mental states. An emotional experience manifests when there is resonance across levels, that is, concrete features are made meaningful as a conceptualization of a discrete emotion category, in a given context. Without higher levels making meaning of lower levels, elemental concrete features (e.g., tachycardia), or combinations of features (e.g., tachycardia and hindlimb locomotion), are not necessarily a manifestation of an emotional experience. Without top-down categories and conceptualizations [63,120,126,128], an instance of features may be experienced in alternative ways, for example, as merely a behavior (e.g., running), visceral sensation (e.g., stomach sinking), or general affective feeling (e.g., displeasure) [131]. A single conceptualization may be formed on the basis of regularities across instances, a capacity that may be shared with non-human animals (e.g., a particular situated conceptualization involving a predator–prey interaction). However, the capacity for higher levels of abstraction, including forming emotion categories from multiple conceptualizations and thus having the ability to generalize across diverse instances of fear, may be more unique to humans.

Figure I (bottom) portrays how emotion representations vary in granularity, or the extent to which emotions representations are more or less discrete. The term granularity typically refers to between-category granularity (e.g., distinctness of anger from disgust). Here, low versus high granularity refers to when there is more or less overlap, respectively, in the representational space of the emotion categories. There could also be within-category granularity: the representational space for a single emotion category, such as fear, may involve a single conceptualization (left), or more complexly, two or multiple situated conceptualizations. Thus, the representational space within a single emotion category may provide a better or worse fit to instances in a multidimensional space. Worse fits imply that the situated conceptualization is used as a 'blunt instrument', driving a person to make the same sort of predictions and engage in the same sort of behaviors across heterogeneous instances (e.g., avoidance, regardless of whether a situation involves heights, social evaluation, or a predator). A better fit implies that the conceptualization better matches a given instance to drive contextually appropriate predictions and behaviors. Granularity is develops across the lifespan [99,132] and relates with mental health (for related constructs of levels of emotional awareness and alexithymia, see [131,133]).
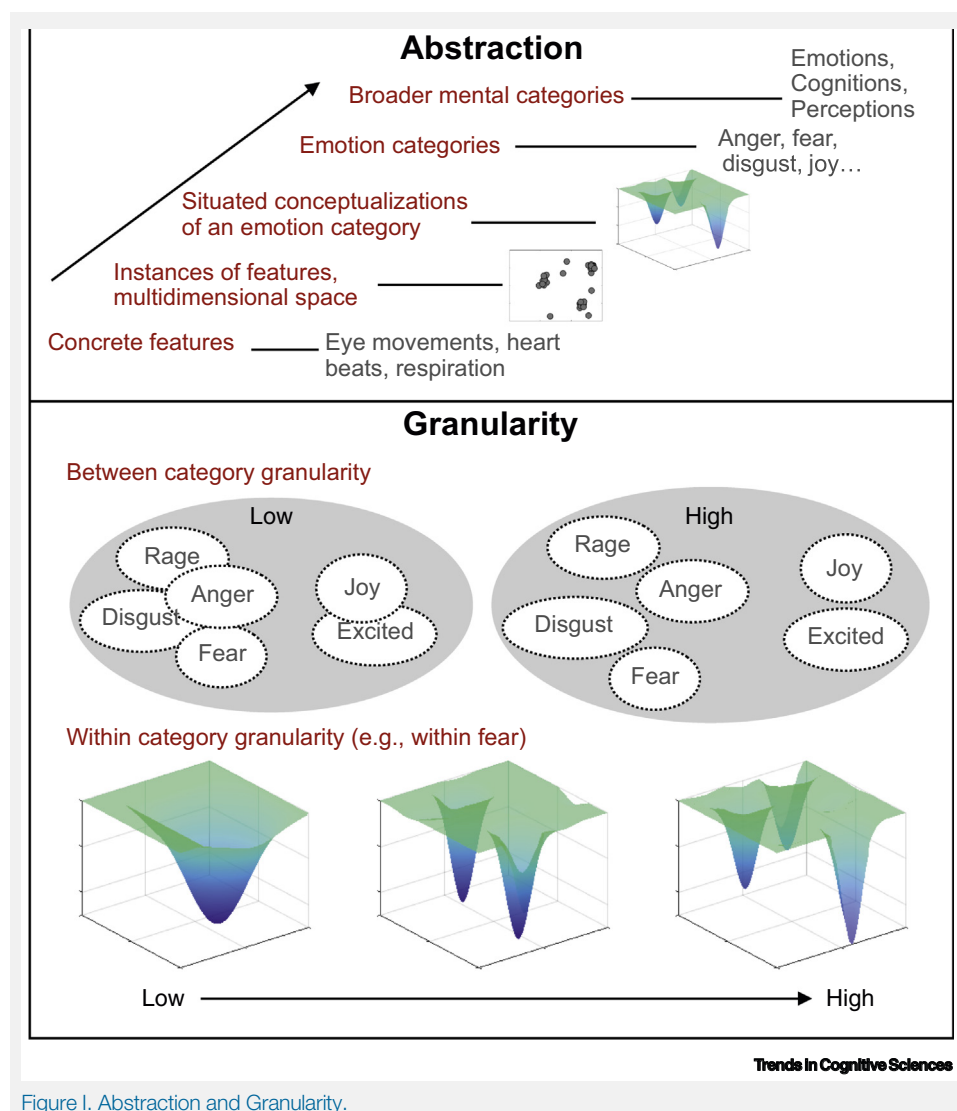
Figure I. Abstraction and Granularity.

general psychological and neural mechanisms. Like emotional experiences (Box 1), a given category for emotion perception often involves collections of instances with high within-category variability [23]. Perceptions of discrete emotions involve abstracting across diverse inputs (visual inputs such as faces and bodies, auditory inputs such as vocalizations, etc.) and conceptualizing them as instances of a discrete emotion category. Thus, emotional experience and emotion perception share the ability to abstract across instances with heterogeneous features, which we suggest involves the DMN.

Multiple studies have shown that DMN nodes are important for the ability to differentiate discrete emotions in facial expressions. For instance, one study examined emotion perception deficits in 71 patients who underwent tumor removal throughout the brain [60]. Impaired ability to perceive discrete emotions in facial expressions correlated with lesions in DMN areas including bilateral anterior temporal cortex and temporal poles. Similarly, a case study of three semantic dementia
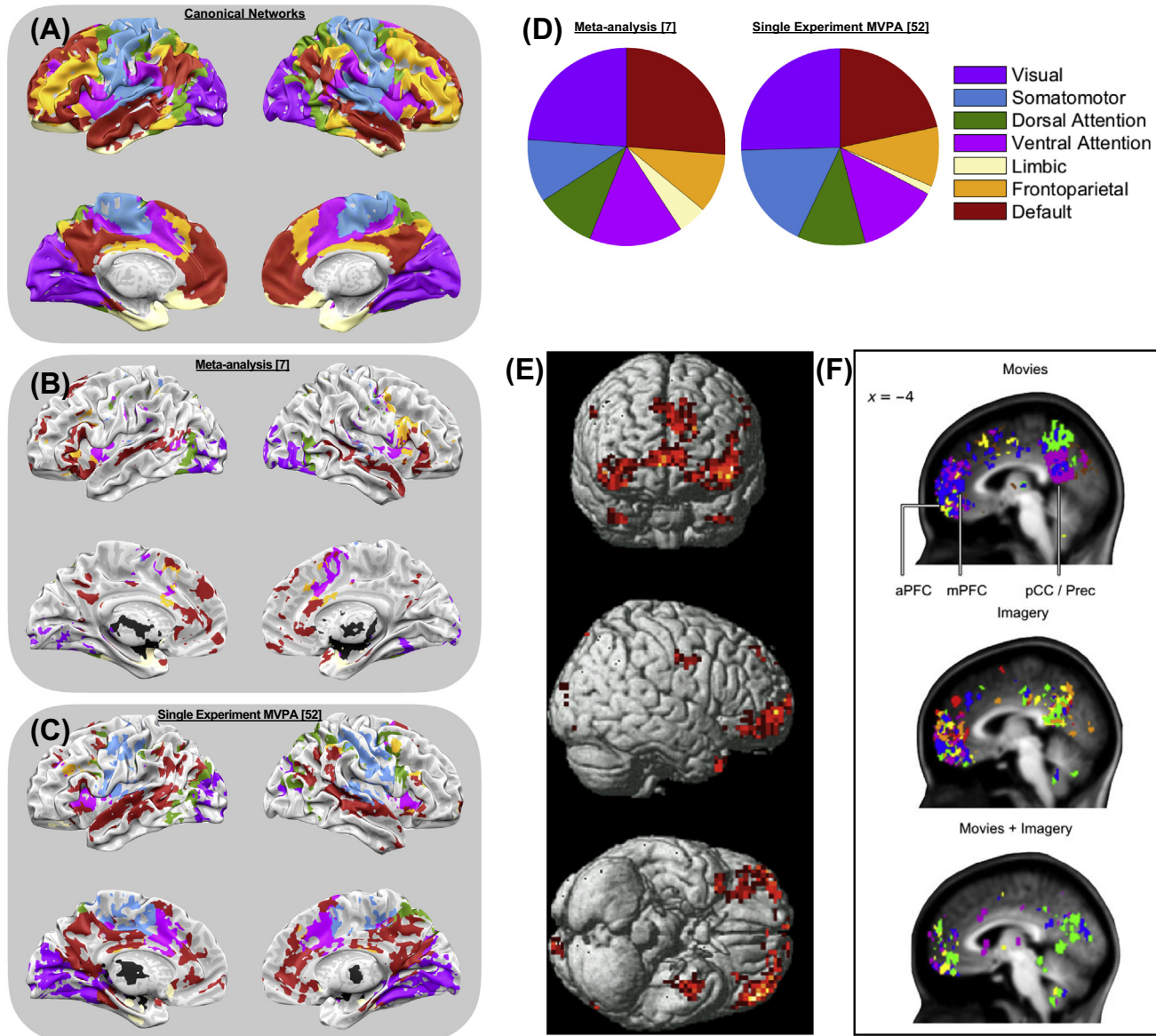
Figure 1. The Default Mode Network (DMN) and Multivoxel Pattern Analysis (MVPA) Studies of Emotion. Four MVPA studies show that voxels contributing to emotion classification are widely distributed throughout the brain. (A) The canonical functional network architecture for reference [19]. (B) Voxels reliably engaged during discrete emotions from a meta-analytic database [7], color coded by location in the canonical network scheme (DMN = red). (C) Voxels informative for decoding discrete emotional states in a single study [52] where 32 participants were induced to experience seven states (anger, fear, sadness, amused, surprise, content, and neutral). Voxels are again color coded by location in the canonical network scheme. (D) The pie charts show that across both a meta-analysis [7] and single study [52], voxels that decode emotion categories tend to be similarly distributed across canonical networks and with a substantial portion residing in the DMN. (E,F) For two studies [14,46], we were unable to obtain statistical maps to examine the exact overlap with the DMN, and therefore we only illustrate their findings here. Visual inspection shows, again, that voxels contributing to emotion classification are present in the DMN, for example, in the anterior medial prefrontal cortex and posterior medial complex. Notably, in two of the four studies there is also prominent involvement in occipital cortex. Our network model suggests that multiple networks contribute to emotion classification, albeit play different roles. The visual network, for example, may represent information that is closer to more concrete feature levels (Box 1; see supplemental information online for a discussion). Abbreviations: aPFC, anterior prefrontal cortex; mPFC, medial prefrontal cortex; PCC, posterior cingulate cortex; Prec, precuneus.

patients with left anterior temporal lobe damage [49] found that patients had difficulty perceiving facial stimuli as expressions of discrete emotions. Participants were asked to sort faces into piles with similar expressions. Rather than sorting them in discrete emotion categories (like healthy controls), they sorted faces into piles representing pleasant, unpleasant, and neutral affect. Another study examined emotion perception deficits in 16 patients with frontotemporal dementia [48] and found that impaired ability to identify that an emotionally expressive gait was emotional versus neutral was associated with lesions in the anterior temporal lobe, whereas impairments in correctly categorizing the discrete emotion expressed was associated with lesions in the IFG. Similarly, an inability to differentiate between different discrete emotions in 44 patients with frontal lesions was most associated with IFG lesions [42], as was emotion differentiation in a separate study of 61 patients with multiple sclerosis [61]. Finally, 180 traumatic brain injury patients with impairments in understanding discrete negative emotions (e.g., differentiating anger from disgust) were most likely to have lesions to a broad swath of DMN regions including: medial prefrontal cortex, bilateral IFG, bilateral medial frontal gyrus, bilateral middle frontal gyrus, and left STG [62].

Taken together, the available imaging, electrical stimulation, and lesion work suggests that the DMN plays a constitutive role in creating discrete experiences and perceptions of emotion. Next, we offer a theoretical account for why the DMN, a network linked to seemingly distinct constructs such as semantics, autobiographical memory, mental time travel, theory of mind, etc. [18,29,30,33,34], is playing a role in constituting experiences of anger, fear, and disgust.

DMN Supports Abstraction in Emotion

We [4,21] and others [24] have suggested that the DMN may be involved in emotion by supporting conceptualization (Box 1). Conceptualization is the predictive process by which prior experiences and knowledge is used to make meaning of more concrete features [25]. Doing so requires generation of an internal prediction about the meaning of internal and external sensations and behaviors given the present context [25]. Conceptualization extends across levels of abstraction [63], spanning across sensory features, multimodal sensory information, and more abstract levels (e.g., dimensions of meaning [64,65]). We specifically propose that the DMN plays a role in representing discrete emotions because it abstracts across instances with heterogeneous features (Box 1).

The neuroanatomical properties of the DMN support its role in abstraction. Research on comparative neuroanatomy of the isocortex [66] has shown a gradient in the neuronal density [67,68] and connection distance in the isocortex [69,70]. Early sensory areas such as V1 have a high neuronal density and low connection distance. This architecture is well suited to represent concrete features in multitudes (i.e., high dimensional space). In comparison, the DMN has lower neuronal density and higher connection distances. This architecture positions the DMN to represent instances of features more abstractly as situated conceptualizations, and engage in the higher levels of abstraction that are important for generalization across diverse conceptualizations. As noted in [66], the gradient in isocortex supports dimensionality reduction. DMN nodes are thus neuroanatomically positioned to enable low-dimensional, compact representations in neural information processing that may support phenomena requiring higher levels of abstraction in psychological representations.

This neuroanatomical view of DMN function is also bolstered by functional findings. The DMN shows greater activity when individuals perform tasks that require greater abstraction. DMN nodes including the anterior medial prefrontal cortex, hippocampus, and precuneus show greater activity when incidentally learning abstract relationships in a simple associative learning task (i.e., learning that transcends simple, elemental associative learning [71]). Several DMN nodes

also show greater activity when people conceptualize the exact same social stimulus at increasingly higher levels of abstraction [e.g., from conceptualizing the exact same features shown in a video clip more concretely as a person covering their face with their arms, to more abstractly as cowering, or even more abstractly as fear (Box 1)] [72,73]. The role of the DMN in abstraction is also supported by its role crossmodal semantic processing, which requires abstracting semantic meaning across more concrete, modality specific features [74]. Relatedly, areas that support higher levels of abstraction are also likely to be the furthest away from early sensory areas. Consistent with this notion, DMN nodes were observed to be the most functionally distant regions in the brain from the early sensory cortices using a stepwise functional connectivity analysis of neuroimaging resting state data [75].

It is tempting to assume that by abstraction, we mean a cognitive process that is distinct from affective processes such as emotion; however, this division is neither the intent of our theory (i.e., conceptualization includes an integration of both external and internal features [4,24,25]) nor is it strongly reflected in the brain. Tract tracing and functional connectivity studies suggest that the DMN and salience network share hubs in the thalamus, hypothalamus, amygdala, and ventral striatum; areas that themselves control visceral activation [76,77]. The DMN is also intimately related with brainstem nuclei crucial for driving autonomic activity and arousal [77,78]. Increased connectivity occurs between DMN and salience nodes during discrete emotions [13,79] and may reflect information processing as DMN uses conceptualizations (i.e., draws on prior experience and knowledge) to drive somatovisceral activity in a given context. Consistent with this hypothesis, DMN nodes are involved when making contextually sensitive escape behaviors [80] and drawing on contextually sensitive prior experiences [81]. DMN areas are also more strongly involved as the demand to resolve a situated conceptualization increases, such as when experiencing atypical instances of an emotion category, such as 'pleasant fear' [82], experiencing an unpleasant feeling as the atypical approach state of 'morbid curiosity' [83], or when having to assimilate continuously varying and ambiguous feelings into more discrete emotion concepts [84]. Highlighting the abstraction involved in conceptualization, DMN activity captures the commonalities amongst multiple instances of a highly situated emotional experience (e.g., anger) across multimodal induction methods [46,85], and the higher-order dimensions of meanings people attribute to emotional situations [64,65]. These findings are consistent with the idea that the DMN drives autonomic and visceromotor activity to be situationally appropriate with respect to the more abstract adaptive themes associated with a given emotion category.

Novel Predictions and Future Directions

The proposed theoretical framework for the role of the DMN in emotion representation leads to a set of novel predictions (see Outstanding Questions). For instance, our approach has predictions for when the DMN is more or less in demand due to phylogenetic and ontogenetic variation, individual variation, and variation due to disease (Box 2).

When discussing the role of the DMN in human emotion, a relevant question is whether the neural architecture for emotions is functionally conserved across individuals and species, and if so, whether the DMN plays a similar role in emotion in human and non-human animals. The extent to which the neuronal architecture for emotion is evolutionarily conserved is a topic of contentious debate [86–90], with researchers varying in the extent to which they emphasize species-conserved adaptive behaviors (e.g., freezing) versus the multitude and diverse situations in which humans feel emotions. Humans and non-human animals alike engage in adaptive behaviors in some threatening contexts [90]. There is also evidence for a default mode in non-human animals such as rodents [91], non-human primates [92], and human infants, although there is both important phylogenetic variation and ontogenetic variation in the functional architecture of the DMN

(e.g., mouse DMN has less densely connected nodes than the primate DMN, [93]; human infants have less densely connected nodes than children or adults, [94]). The relevant question is whether human emotions involve more than just the instances in which an adaptive behavior is evoked and relatively how much the DMN contributes to the features of emotion beyond adaptive behaviors.

A novel prediction of our approach is that the role of the DMN in emotion may vary across species and in human development. Adult humans sometimes freeze during fear, but many instances of fear do not involve freezing, meaning that adult humans may need to abstract and generalize their situated behaviors across a wider range of threatening contexts. In contrast, most non-human animals experience a limited set of predators in their species-typical environments and situations vary in relatively constrained ways (predators are either absent, looming, or striking [95]). Whereas in humans, DMN nodes carry information for classifying emotional categories across diverse concrete features (faces, bodies, situations, etc. [64,96]), it is unclear whether the same is true for non-human animals. Human infants also experience a limited set of threats in their earliest months, most of which they cannot control. To the extent that a non-human animal needs to generalize to a novel context (e.g., a novel predator, a species-atypical context), or to the extent that human children experience an increasing array of emotional contexts over the course of early childhood, then the DMN may become relatively more important for acquiring and producing conceptualizations that resemble adult discrete emotions. Consistent with these hypotheses, the DMN exhibits developmental changes in structure over early childhood to adolescence [97], a time that coincides with the development of more differentiated and abstract emotion concepts [98–100].

Our approach also makes important predictions for the involvement of the DMN in adult humans. Individuals vary in emotional granularity (Box 2), or how discrete and complex their emotion representations are. High granularity individuals are better able to separate instances that share common features (e.g., negativity) such that emotions are experienced more discretely. This ability may relate to DMN function and the tendency to employ DMN during emotions. Similarly, failure to activate DMN may occur in individuals who are low in emotional granularity. At the extreme, these individuals are characterized as alexithymic and do not experience their emotions as discrete instances, but as somatovisceral sensations. Preliminary evidence suggests that the DMN is more cohesive in individuals who experience their emotions in a more complex manner [101], and is less cohesive for individuals high in alexithymia [102,103]. A wealth of research also links DMN dysfunction to emotional dysfunction [31,32]. Future research might explore whether individuals with DMN dysfunction also show differences in emotional experience in terms of granularity or abstraction. Studies of autistic individuals may be illustrative, as autistic individuals have deficits in DMN structure and function [104], and tend not to experience highly differentiated discrete emotions [105]. As compared with neurotypical children, highly functioning autistic children focus more on the high dimensional details of emotional situations (e.g., behaviors, events), without abstracting to the hierarchical emotional meaning of that situation (e.g., someone felt sad) [106].

Future research may also benefit from unpacking the DMN in greater detail. A closer examination of the structural properties of each node (e.g., cytoarchitecture) suggests that DMN nodes may support different aspects of conceptualization or degrees of abstraction. DMN nodes also link memory with visceral regulation [78,107], which our view suggests is important for constructing discrete emotions (Box 1). Recent work on the biological mechanisms that create large scale functional networks [108,109] may also be of interest for future network models of emotion.

Concluding Remarks

The function of the DMN has been the topic of debate since its discovery approximately 20 years ago [18]. Here, we review the existing neuroimaging, intracranial stimulation, and lesion evidence,

Outstanding Questions

Does the degree of abstraction and conceptualization demanded by a situation predict DMN engagement in discrete emotions?

Do causal manipulations of the DMN qualitatively change experiences of discrete emotions? For example, do disruptions to DMN function interfere with the generalization of instances of an emotion category across situations?

How do differences in DMN function and structure across early development relate to the acquisition, abstraction, and granularity of discrete emotions?

Do differences in DMN function or structure predict perturbations in emotion representation in clinical disorders?

Can we predict the involvement of different DMN nodes in discrete emotions on the basis of their functional and anatomical properties?

How do we create a computational model of the neural basis of feeling an emotion if there are many different behavioral, cognitive, and physiological patterns that relate with the same emotion across different situations?

Given a set of patterns that predict fear in the human brain, do non-human animals exhibit analogous neural patterns of activation in situations involving defensive behavior?

MVPA studies of emotion engage multiple functional whole brain networks including the occipital cortex. Does the occipital cortex mainly contribute to emotion differentiation when the emotion-discriminant features are more concrete and visually-related? Is functional connectivity between the DMN and the occipital cortex important for emotion differentiation in these cases?

and offer the hypothesis that the DMN is constitutive of discrete experiences of emotion. Building on a constructionist theory of emotion, we summarize how the DMN holds representational content for discrete emotions because it helps an individual make meaning of his or her affective sensations in light of the present context by drawing on a pool of prior experiences. This process involves abstraction, which the DMN is well suited to support based on its structural and functional anatomy. If the DMN is important for enabling abstraction, then there should be less DMN involvement when abstraction is less needed to create an experience of emotion, and loss of DMN integrity may impair the experience of emotions as discrete and the ability to generalize across diverse instances of an emotion category. Our theoretical framework of relating abstraction and granularity to emotion representation thus may lead to new directions for understanding how emotions vary across species, and also how emotion and DMN functionality relate with emotion representation across individuals.

Supplemental Information

Supplemental information associated with this article can be found online at https://doi.org/10.1016/j.tics.2019.07.003.

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