Trends in Cognitive Sciences

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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.**

## 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.

## 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

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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

## 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