



## Review article

## Emotions as discrete patterns of systemic activity

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## HIGHLIGHTS

- Emotions automatically organize human and animal behaviour.
- We review recent pattern recognition studies on human emotion systems.
- The data suggest categorical structure of emotions across multiple domains.
- Discrete emotion systems are organized in a distributed fashion across the brain.

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## ABSTRACT

Emotions organize human and animal behaviour by automatically adjusting their actions at multiple physiological and behavioural scales. Recently, pattern recognition techniques have emerged as an important tool for quantifying the neural, physiological, and phenomenological organization of emotions in humans. Here we review recent advances in our understanding of the human emotion system from the viewpoint of pattern recognition studies, focussing on neuroimaging experiments. These studies suggest, in general, clear and consistent categorical structure of emotions across multiple levels of analysis spanning expressive behaviour, subjective experiences, physiological activity, and neural activation patterns. In particular, the neurophysiological data support the view of multiple discrete emotion systems that are organized in a distributed fashion across the brain, with no clear one-to-one mapping between emotions and brain regions. However, these techniques are inherently limited by the choice of *a priori* emotion categories used in the studies, and cannot provide direct causal evidence for brain activity-emotion relationships.

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## 1. Introduction

Emotions organize our lives by automatically orienting actions and modulating approach-avoidance motivation [1,2]. Currently, there exist multiple neurophysiological and psychological models for emotions. A shared assumption of all of these is that emotions are best understood as modulatory systems that interact with both “lower-order” (e.g. homeostatic and motor) and “higher-order” (e.g. cognitive) systems for adjusting decision making and survival odds. What is however hotly debated is how these modulatory emotion circuits are organized in the brain. Categorical models of emotions argue that evolution has shaped a limited set of basic emotions (usually including anger, fear, disgust, happiness, sadness, and surprise) with distinct neural and physiological substrates to support specialized survival functions [3,4]. These basic emotions are also characterized by distinctive subjective feelings (such as “I feel happy”), culturally universal expressions, and possibly also discrete functional neural basis [5–8]. However, it has also been proposed that behavioural, physiological and subjective bases of emotions should be understood in terms of a limited number of general-purpose systems; typically one governing pleasure versus displeasure (often coined valence) and the other calmness versus arousal. The relative activity of these systems could then generate different patterns of emotional behaviour and experiences [2,9]. The distinctions between the proposed different emotion systems as well as their innateness have been a matter of sometimes even fierce debate. Here we review how studies using multivariate pattern recognition techniques used on various levels of behavioural, physiological and neural data have advanced this discussion.

## 2. Multivariate pattern recognition

Multivariate pattern recognition is an umbrella term for a variety of machine learning techniques focused on learning regularities or patterns in the data, thus allowing analysis of discriminability and specificity of data patterns across different classes or conditions [10]. In the context of psychology and neuroimaging, the greatest advantage of these techniques is that they focus on distributed activity patterns rather than mean regional intensity changes (c.f. conventional GLM) that a system such as brain or autonomous nervous system can produce. Consequently, they significantly increase the amount of information that can be decoded from the system under scrutiny [11]. Typically, this type of analysis involves implementing a machine learning algorithm that tries to learn associations between a set of *a priori* categories and the multivariate data profiles associated with them. If the differences are consistent, they should be reproducible in independent samples, thus the generalizability of the algorithms is typically tested by evaluating their performance against independent datasets that were not used in training the algorithm.

Pattern recognition analyses are theoretically well-suited for tackling the organization of human emotion systems for multiple reasons. First, they are inherently focused on analysing system-level patterns, which are also a central tenet of most emotion models. Second, successful classification of two or more emotional states would require that they elicit consistently different activation patterns, thus allowing testing the discreteness of different emotional states. Third, successful cross-validation of the classifier across independent samples of subjects would require consistent emotion specific activations across individuals,<sup>1</sup> possibly providing evidence for the biological versus acquired basis of emotions.

<sup>1</sup> Yet due to individual variations in anatomy and functional specialization, this may require functional realignment of the neural data across subjects to be successful [12]

Fourth, investigating the similarities and distances of the emotion-evoked patterns across a large array of emotions allows revealing the (categorical or dimensional) structure of the emotion space.

## 3. Emotions as discrete activation patterns at multiple levels

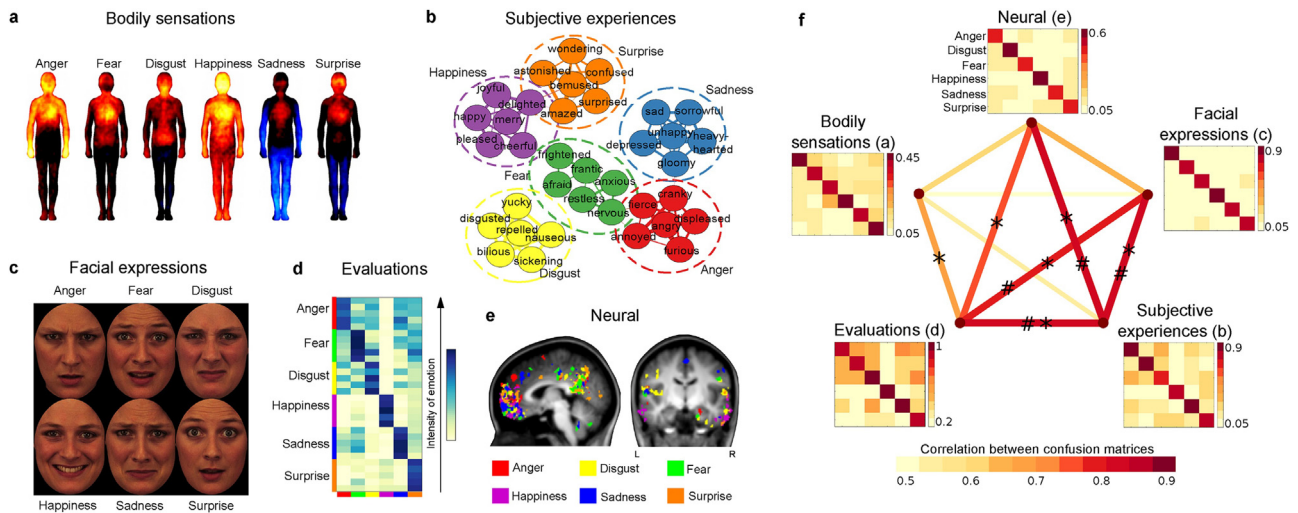
### 3.1. Emotional expressions

The concept of discreteness and “basicness” of emotions stems from Paul Ekman’s group’s pioneering work revealing that a limited number of facial expressions are used consistently to communicate emotion in diverse array of different cultures [13]. The facial expressions were proposed to be driven by distinct neurophysiological emotion systems, and this assumption of discreteness has guided much of subsequent work on the nature of human emotions. Although the strong variant of cultural universalism in expressions has been challenged [14], studies have consistently established that facial expressions of emotions are perceived as discrete entities, with clear category boundaries between individual expressions [15,16]. As these boundaries are seen even when the subjects do not have appropriate lexical categories for the emotions, facial expression perception is likely driven by biologically evolved systems, rather than pre-established lexical labels [17]. Similarly, there is evidence suggesting categorical and universal expression and perception of emotions in other modalities, such as vocalizations [18]. Importantly, also neurocomputational facial expression recognition models [19,20] place similar category boundaries between morphed facial expressions, and show similar patterns of confusion between expressions as human observers, further supporting discreteness of emotional expressions.

Functional magnetic resonance imaging studies using multivariate pattern recognition analysis have established discrete neural signatures for perceived emotional facial [21,22], bodily [22] and vocal [22–24] expressions. These expression-specific signatures are typically observed in the corresponding sensory cortices but also in larger networks of interacting cerebral regions. These sensory representations are also supramodal [22,25], and physical similarity of the emotional stimuli (such as two facial expressions) is also reflected in the similarity of the corresponding neural activity patterns [21]. All in all, these emotion-specific perceptual codes accord well with the behavioural findings and computational modeling work on perceptual categorical structure of emotional signals.

### 3.2. Subjective feelings and physiological responses

One implicit reason for the strong focus on discreteness of different emotions is the way we subjectively – as scientists and laypersons – experience the states we call emotions. Different emotions simply feel qualitatively different at phenomenological level: “Being sad” is experienced as a clearly distinct mental state than “being happy” [7,26]. This discreteness also extends to the emotion-dependent bodily responses, often assumed to underlie subjective emotional feelings [27,28]. Quantitative meta-analytic evidence shows that different emotions evoke distinct patterns of autonomous nervous system (ANS) activity [8], also leading to quantitatively discrete “feeling fingerprints” in the body [6,29]. Both the subjective bodily sensations triggered by each emotion [6] as well as their underlying physiological signals stemming from sympathetic/parasympathetic branches of ANS [30–32] can be reliably classified using pattern recognition techniques, again providing evidence for specificity of discrete emotion categories. However, these studies have been done with relatively coarse indices of ANS and skeletomuscular activity, and detailed and regionally specific whole-body data on emotion-dependent



**Fig. 1.** Discrete representations of emotions in (a) self-reported bodily sensations [6], (b) subjective experience [7], (c) facial expressions [46], (d) intensity profiles of basic emotion ratings for short emotional narratives [6], and (e) neural responses based on voxels contributing most significantly to accurate MVPA-classification of basic emotions from BOLD-fMRI data [7]. (f) Confusion matrices and the crossmodal similarities (Spearman correlations) between bodily cognitive-evaluative, subjective, expressive, and neural representation of emotions. The modality-wise confusion matrices are based on Linear Discriminant Analysis (LDA) classifier run on the bodily maps of emotions (a), direct pairwise ratings of emotion concepts (b), human observers' confusions between facial expression categories (c), Euclidian similarity of intensity profiles of discrete emotion ratings for short narratives (d), and confusions of a pattern classifier (MVPA) on BOLD-fMRI data (e). Line strength denotes crossmodal similarity between two matrices, all shown crossmodal similarities are significant ( $p < 0.001$ ) in a parametric test. Asterisks (\*) denote significant similarities in a complementary permutation-based test where values were obtained by permuting the row and corresponding column elements, followed by BH-FDR correction [63]. Hashes (#) indicate significant similarities in analysis where diagonal elements were excluded from the matrices. Elements a–e reprinted with permission from [6,7,64].

skeletomuscular, visceral and cardiovascular responses is currently lacking.

### 3.3. Emotional responses in the central nervous system

A large bulk of animal studies has delineated discrete neural circuits for different basic emotions or affect systems (see review in 33). In line with this, initial patient studies suggested that focal brain damage leads to impaired recognition and experience of specific emotions in a regionally selective manner [34,35], supporting the idea of discrete and anatomically separable emotion systems in the brain. However, accumulating evidence from neuropsychological studies on patients with focal brain damage has not conclusively supported one-to-one mapping between specific brain regions and specific emotions [36]. Similarly, results from human neuroimaging studies using univariate analysis have been inconclusive in this respect. Some meta-analyses have found support for discrete brain basis of basic emotions [37–39] whereas others have challenged this notion [40], and some reaching more intermediate conclusions [41]. Yet, it is also possible that differential activation patterns for each basic emotion exist in the subcortical emotion circuits and their cortical extensions, but remain uncovered with the univariate analyses suffering from the poor spatial resolution of the routinely used echo-planar sequences in 3 T MRI.

One line of pattern recognition studies has focussed on actual emotional states rather than, for example, sensory activations triggered by seeing emotional expressions. These studies have confirmed that both sustained emotion-dependent states of brain activity [7,30,42,43] or spontaneously occurring emotional states during resting state [44,45] are associated with discrete neural activation patterns across different basic and non-basic emotional states. These patterns are consistent across subjects and means by which emotions were induced, and also present in the evolutionary old affective circuits such as in the amygdala [7]. Importantly, these studies have established a strong correspondence between the subjectively felt emotions and their underlying neural activation patterns. The more similar brain activation patterns are for two emotions, the more similar we experience them to be at the subjec-

tive level. These neural signatures thus reflect the net state of the emotion system, which may then be accessed consciously for generating the subjective emotional feeling [7]. However, similarly as patient work [36], these studies provide no support for direct one-to-one mapping between different emotions and different brain regions. Instead, they suggest that emotions are best understood as global large-scale changes in brain activity across subcortical and cortical circuits.

### 3.4. Representational similarity of emotions is consistent across multiple domains

Studies reviewed above provide considerable evidence for expressive (i.e. facial and vocal expressions), experiential, physiological, and neural discreteness of emotions. Different levels of measurements such as autonomous and central nervous system activity as well as subjective experience are however rarely combined in a single study. Yet, because each emotion leads to unique discernible activation pattern across central and peripheral nervous system, analysis of typical confusions or similarity judgments made by human subjects or pattern classifiers in different tasks is informative in revealing whether the representational structure of different emotions is consistent across modalities. To illustrate this, we extracted confusion matrices for neural [7], cognitive-evaluative [6], experiential [7], expressive [46], and bodily [6] signatures of the six basic emotions from three prior studies, and computed the statistical correspondence (Spearman correlation) between the matrices across modalities.

Clear diagonals in the matrices show that the tested emotions are discrete (i.e. confusions among categories are rare) in each modality. Moreover, the general pattern of confusions between emotions is concordant across the modalities in which emotions are measured (Fig. 1). This pattern of crossmodal similarity primarily results from the strong discreteness of emotions in each modality, as most common variance across modalities stems from the difference between diagonal and off-diagonal elements. Although this may be an inherent feature of the similarity structure across emotions, we also re-run the analysis excluding the diagonals from the

matrices thus focussing the analysis on category confusions. The overall pattern of associations remained similar (positive correlations between modalities), yet statistically significant associations were mainly observed between subjective feelings and other modalities, as well as between cognitive-evaluative responses and facial expressions. In sum, the emotions canonically considered as “basic” follow similar pattern of discreteness across multiple levels of analysis, importantly also at the neural level. However, we must next ask how this discreteness should be interpreted particularly in the context of the debate regarding the existence of basic emotions.

#### 4. What pattern recognition studies can and cannot reveal about the organization of emotions

##### 4.1. Pattern recognition analysis is compromised by the *a priori* class labels

Traditional pattern recognition techniques such as MVPA are dependent on the *a priori* class labels. In most approaches the classifier tries to learn and subsequently predict the associations between class labels (e.g. emotions) and dependent measures such as brain activity. Accurate classification thus only reveals that the *a priori* classes can be distinguished from each other on the basis of the data, but does not resolve whether the classes actually comprise of the most accurate representation of the studied process, or whether the data contain a completely different class structure. Showing that basic emotions can be classified from brain imaging data alone thus by no means confirms that these would be the only discrete emotion systems in the brain, or that this classification scheme would be the optimal way to represent human emotions. Also, to our knowledge no prior pattern recognition study has tried dissociating emotions from related processes such as, for example, motivation, hunger, and sexual drive, or tried to characterise the neural organization of multiple emotion states in data-driven fashion without *a priori* category assumptions. Thus, we only know that with the *commonly used class labels* different emotions are statistically discernible, but their neural, bodily, and phenomenological similarity with respect to other physiological and psychological states remains poorly understood. In future, it would thus be imperative to address representational structure of emotions and related motivational and homeostatic states simultaneously across brain imaging, physiological, and subjective measurements.

Conventional fMRI-MVPA analysis is also strictly regional, and it does not consider the large-scale connectivity changes occurring different emotional states. For example, one study revealed that about 3% of all possible voxel-by-voxel connections (394758 out of 13429153) show emotion dependent changes during fMRI [47]. Thus, decoding from the emotion-driven connectivity changes might be a powerful approach for studying organization of the emotion systems [48]. Similarly, analysing the connectivity changes between peripheral and central nervous system could yield novel insights into the mental and bodily organization of emotions. These types of experiments are however challenging to set up in the fMRI because the connectivity models require long BOLD time series and enough variation in the stimulation models; however, naturalistic stimulation such as narratives, music and movies provide a convenient means for prolonged stimulation with variable emotion time courses [49].

##### 4.2. How should we interpret distinct activity patterns elicited by different emotions?

Despite evident success with establishing dissociable neural patterns evoked by distinct emotions [7,30,42–45], an important

question pertains to when successful classification of two distinct emotion states supports the existence of different underlying neurophysiological systems. To take an example from another domain, being able to classify whether subjects have heard the word “cat” or “dog” from BOLD signals recorded from auditory cortex does not obviously prove that distinct neural systems would be involved in processing words “cat” and “dog”. And neither would cross-modal classification of the same words when presented in spoken or written format, because individuals have likely learned to associate spoken and written word forms together, possibly leading to coactivation of both representations upon encountering the spoken or written word. Establishing the consistent crossmodal (e.g. across written and spoken formats) classification across different lexical categories in the absence of learned associations (e.g. in individuals never exposed to written language) would however be more likely interpreted as domain-general, word-specific neural signatures, yet it is obviously extremely unlikely that this could be accomplished. In the context of emotion research similar criteria would involve consistent, successful cross-subject classification of emotions elicited by multiple techniques, and existence of emotion-specific neural signatures in brain systems implicated in emotional processing in animal and patient studies. Unlike in the fictitious example on word processing, this type of crossmodal and cross-subjects classification is actually possible for different basic emotions [7]. However, even then caution is warranted in interpretation, as the pattern recognition technique per se only reveals discriminability and specificity of the neural signatures associated with each emotion, rather than describing the putative emotion circuits at neurophysiological level. More recent analytic approaches allow predicting multivariate neural responses to new stimuli using high-dimensional feature models of the stimuli [50]; establishing similar mapping between emotion-eliciting conditions and the corresponding responses in the central and peripheral nervous system would significantly improve our understanding of the functional mechanisms of emotions.

Emotion systems show also remarkable experience-dependent plasticity. Because most pattern recognition studies have been conducted in adults, it is possible that shared environmental exposure across subjects – rather than innate biological systems – might partially underlie the observed emotion-specific activation patterns. One way to test these assumptions would involve comparing neural signatures of different emotions in infants versus adults. In such cross-sectional framework, successful across-groups classification would provide strong evidence for innateness of the discrete emotion systems.

Finally, the pattern recognition techniques cannot provide truly causal evidence for the existence (or lack of it) of basic emotion systems: Observing emotion-specific activation patterns for specific emotions does not prove that these patterns would be strictly necessary for the corresponding emotional responses. Such causal evidence is however difficult to establish in any human studies. Neuropsychological studies with patients with focal lesions are often limited by the specificity of the lesions and the neuroplasticity of the adult brain [36]. Commonly used human brain stimulation techniques such as transcranial magnetic stimulation [51] cannot reliably and accurately target subcortical structures consistently implicated in primary affective processing in animals [33,52]. Evidence from direct neuronal stimulation studies is still scarce [53,54], and results of systemic-level neuroreceptor agonists/antagonists are also inherently difficult to interpret [55]. Despite methodological advances in signal analysis, both patient studies and animal work are thus critical in advancing our understanding of the organization of human emotions in the future.

#### 4.3. Future pattern recognition work should focus on natural emotional behaviours

Animal studies on emotion are critically dependent on measuring patterns of emotional behaviour such as freezing, licking, and rough-and-tumble play to ensure that an emotion has been elicited in the animal [56]. Yet genuinely behaviour-based studies on human emotions (except their expressions) and attempts to classify them are still surprisingly sparse. Already a decade ago, Roy Baumeister and colleagues expressed their concern that social psychology was becoming a science of button presses and self-reports [57]. Human emotion science has, to some extent, suffered from a similar problem by focusing heavily on sensory processing of facial expressions and emotion-evoking pictures, self-reported emotional states or learning-dependent, reflective emotional processing. Actual measurements of emotional behaviour and emotional responses in realistic situations evoking strong emotions have been notably scarce. However, modern behavioural recoding techniques with, for example, mobile tracking and ecological momentary assessment using cellphones, might provide interesting opportunities for classification of a variety of emotional behaviours occurring in natural conditions.

Finally, many real-life emotional behaviours (such as escape and aggression) cannot be elicited during brain imaging and thus neural recordings of such behaviours in the scanner environment are difficult to accomplish. However, nuclear medicine imaging allows one possibility for their off-line measurement by pre-experimental injection of the radioligand, whose binding can be quantified after the experimental treatment. Such studies have been used to quantify, for example, engagement of Broca's area's homologue during vocal communication in free-ranging chimpanzees [58], and endogenous opioid release following euphoria-triggering physical exercise in humans [59]. The problem of such techniques is obviously their lack of temporal sensitivity, yet they are well-suited for tracking slow-acting or tonic changes in neurotransmission and cerebral perfusion during strong, real-life emotional behaviours and experiences.

## 5. Conclusions

### *Disentangling discreteness and basicness in emotion science with pattern recognition*

Evidence from human studies suggests that basic emotions are discrete across several expressive, experiential, physiological and neural levels. This discreteness is best understood as widespread, system-level patterned activity, rather than selective regional or systemic engagement during specific emotions. This discreteness also poses an intriguing question: Given that different emotions are based on profoundly different activation patterns in the central and peripheral nervous system, is it worthwhile to treat all these systems under the umbrella term of emotion? We think that this tendency stems from the fact that subjective experiences of emotions in the mind and the body are the phenomenologically most salient aspects of human emotions. Even though the neurobiology and behavioural repertoire of pleasure is distinct from that of fear, we tend to, both as laypersons and as scientists, group both responses as *more similar with each other than some other (e.g. cognitive) functions not associated with equally strong subjective sensations*. The concept of *emotions* thus captures effectively states that are so vital to the organism that they leak prominently into consciousness. Thus, emotions feel qualitatively so different from other cognitive and physiological functions, that we are inherently biased for grouping them together for scientific analysis even though the underlying neurobiology between, for example, fear

and pleasure, would be very different. We may indeed be able to better understand different emotions if we focussed on their inherent differences rather than their similarities. Perhaps, one may argue, it would be better to study each emotion and the associated behaviours independently, instead of subjecting the wide variety of differential processes under the same functional category.

Finally, we stress that “basicness” or “discreteness” of emotions are not only purely theoretical questions, as the organization of emotion circuits also has a great clinical impact for effective diagnosis and treatments for affective disorders. For example, if a limited number of lower-order dimensions would support emotions, then pharmacological (or behavioural) up- and downregulation would presumably be a feasible way for treating their disorders. However, both pharmacological experiments and clinical trials suggest that this is not the case. There is evidence of different neurotransmitter systems contributing differently to specific emotional functions [55,60–62], an issue that has however remained relatively poorly understood. Tackling this question requires substantial outreach beyond the widely used functional neuroimaging and electromagnetic recordings. Yet in the future, combining pattern recognition analysis of the emotion circuits at the level of specific neurotransmitter systems measured with nuclear imaging techniques might yield clinically highly relevant information regarding the organization of human emotions.

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