Contents lists available at ScienceDirect

Neuroscience Letters

journal homepage: www.elsevier.com

Review article

The neuroscience of understanding the emotions of others

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ARTICLE INFO

Article history:
Received 16 March 2017
Received in revised form 8 June 2017
Accepted 13 June 2017
Available online xxx

Keywords:
Emotion
Inference
Perception
fMRI
Neuroimaging

ABSTRACT

We cannot help but impute emotions to the behaviors of others, and constantly infer not only *what* others are feeling, but also *why* they feel that way. The comprehension of other people's emotional states is computationally complex and difficult, requiring the flexible, context-sensitive deployment of cognitive operations that encompass rapid orienting to, and recognition of, emotionally salient cues; classification of emotions into culturally-learned categories; and using an abstract theory of mind to reason about what caused the emotion, what future actions the person might be planning, and what we should do next in response. This review summarizes what neuroscience data − primarily functional neuroimaging data − has so far taught us about the cognitive architecture enabling emotion understanding in its various forms.

1. What is emotion understanding?

The essence of emotion understanding is the organization of information around discrete emotion categories. We regularly infer emotions from seeing somebody's facial expression, from hearing an animal's cries, from observing the way a person behaves in a crowd, or even just from reading a situation that a character is facing in a novel. These are all very different types of information, yet all can be made sense of by being classified into an emotion category. We refer to information of this kind as *emotion-relevant*. Typically, we have multiple such types of information available at the same time. To assign a category, such information must somehow be aggregated, with conflicts resolved, to arrive at an emotion category that is most consistent with the sensory evidence available.

We distinguish in our review processes for detecting and orienting attention to emotion-relevant sensory cues in the environment (*detection*); processes for classifying information in emotional terms (*categorization*); and processes for attributing the categorized emotion to a cause (*causal attribution*), often through combination with other forms of social cognition, such as the representation of place-specific social norms and reasoning about mental-states [31,11,34]. As displayed in Fig. 1, these three kinds of process can be conceived as yielding emotion understanding at different levels of abstraction, from a relatively shallow representation of concrete nonverbal cues (e.g., "eyebrows raised toward midline"), to a relatively higher-level representation that combines these cues to infer the emotion category describing *what* the target is feeling (e.g., "fear"); and finally, to an even deeper appreciation of *why* the target feels that way (e.g., "delivering a speech in an hour") [45]. The rather heterogeneous literature germane to emotion understanding, and the correspondingly heterogeneous and unreliable neuroanatomy it has identified, can profit by acknowledging this representational diversity in how humans come to understand stimuli with emotional content. This scheme also makes specific predictions about how this might differ in animals, who may share with us the ability for low-level representations, but lack some of the high-level inferences.

The serialized scheme in Fig. 1 is of course in reality considerably more complicated in at least two ways. For one, all three of the stages depicted in fact typically occur in parallel and overlap in time. Indeed, emotion categorization and attribution can occur extremely rapidly: electrophysiological responses in prefrontal cortex [21], and in the amygdala [27], that differentiate emotion categories inferred from visual stimuli have been reported with latencies around 100 ms, as fast or faster than latencies required for object recognition. Relatedly, there is evidence for multisensory integration at even some of the earliest processing stages—for instance, subcortical structures like the superior colliculus and thalamus already show neuronal responses that integrate visual and auditory information [15,26], and integration of emotional information can again be seen as early as 100 ms with ERPs [30]. This raises the second complication: all arrows in Fig. 1 should be bidirectional, and there is good evidence that even high-level attributional representations (e.g., in prefrontal cortex) can feed back down to regions involved in detection and early perception (e.g., in visual cortices). This feedback is in line with computational architectures that emphasize predictive coding and Bayesian inference in perceptual cognition. This is a large subfield of computational neuroscience, in which several different models are being explored for their explanatory power in describing how the brain minimizes sensory errors given prior expectations − and one

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http://dx.doi.org/10.1016/j.neulet.2017.06.018
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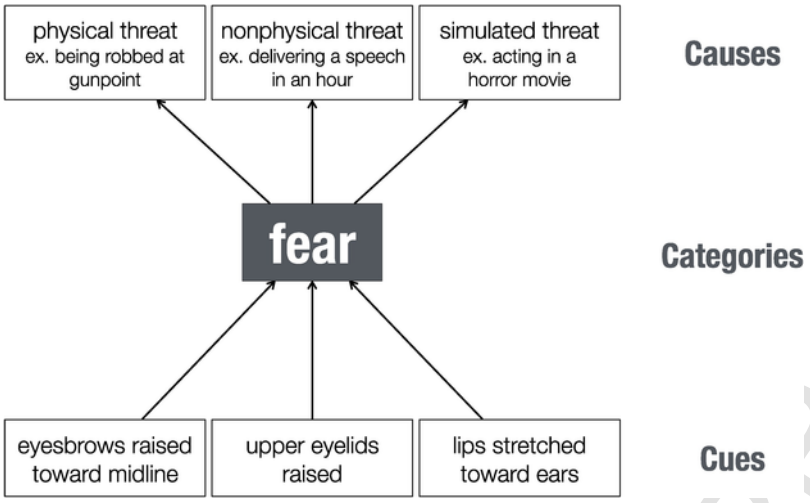

Fig. 1. An illustration of the hierarchical and multifaceted nature of understanding other people's behavior in emotional terms. We use fear as an example, but note that the distinctions we make can be applied to any emotion category. To simplify, we demonstrated how a fearful facial expression might be identified at three levels of abstraction. At the lowest level are the different elements of the stimulus (e.g., facial and bodily actions, object of gaze) that in combination can be understood in terms of relatively higher-level behavioral categories, such as fear. Using our capacity for reasoning about the causes of behavior (e.g., using a Theory of Mind), even higher levels of understanding become possible: We understand not just that the person is expressing fear, but why they are expressing it. To organize the literature review shown in the main text, we compartmentalize component processes as contributing primarily to either early detection of emotion-relevant cues; intermediate categorization of the behavior in terms of emotion and action categories; and, finally, further inferences that serve to build a coherent narrative that identifies the cause(s) of the emotion. In actuality, processing at these three levels is typically concurrent and involves substantial feedback, not shown in this figure.

strategy may be to generate rough prior expectations very rapidly, and then refine them once sensory processing is complete.

Although we focus on emotion understanding from observing other people, such as seeing their facial expressions, as we noted above we regularly infer emotions also from mere descriptions of the situations in which people might find themselves. Several of the studies we mention below (e.g., [37] in fact use such stimuli—lexical descriptions of scenarios from which we would infer an emotion. For example, imagine being told that a child badly wanted a puppy, and one day after school there is a new puppy at home that the child meets for the first time. There is no mention of any observable behavior on the part of child at all, yet this situation is as prototypical as a facial expression and we have no difficulty inferring "happiness" as the emotion. In this example, we do not engage all of the levels of processing shown in Fig. 1: we are able to achieve emotion understanding even in the absence of detection of observable sensory cues. Nonetheless, information about the emotion that can be inferred from this description is represented in the same network of brain structures as for inferring emotions from visual stimuli that show people's behavior [36]. Given the diversity of naturalistic settings in which humans interact and communicate their emotional states to one another, the actual cognitive processes involved in any given instance of emotion understanding will thus vary as a function of the stimulus.

2. Is there emotion? Detecting emotion-relevant cues

People and animals have evolved mechanisms for rapidly detecting the presence of emotional information in the environment. While many of these cues signal information most relevant for the observer (such as potential threats), there is also evidence for detecting a broader array of sensory cues that can serve as building blocks for constructing an emotion understanding of other people. For example, a recent study used multivoxel pattern analysis (MVPA), a multivariate classification approach that distinguishes stimulus categories by patterns of activation measured across many voxels, and found that the right posterior superior temporal sulcus (pSTS) contained reliable information about the presence of different facial actions (such as raising the inner corners of the eyebrows) that provide the basic action units that, when combined, form distinct emotional expressions [43].

Similarly, there is a line of work encompassing lesions [3], single-unit recordings [32], and fMRI [12] suggesting that the amygdala may be particularly sensitive to wide eyes in faces that may signal fear. The eye region of the face tends to draw the observer's visual attention; this attentional bias correlates with amygdala activity in healthy adults and is reduced in patients with amygdala lesions, who also show a corresponding deficit in recognizing fear in facial expressions [3]. There are analogs in other sensory modalities; for instance, screams and cries possess a specific acoustic ingredient—power modulations in the 30–150 Hz range—that imbues them with the emotional quality of "roughness" and also activates the amygdala [5]. There is ongoing debate about the extent to which such cue detection, and in particular the amygdala's role in it, is automatic and non-conscious (e.g., [29].

3. What are they feeling? Identifying specific emotions

Specific cues can serve to direct our attention to information that is salient for emotion understanding, yet by themselves they typically underconstrain the interpretations that are possible. Somebody might also be screaming or wide-eyed after having won a big prize, rather than in anticipation of being eaten by a tiger. Whereas emotion-relevant cues may thus map onto coarser dimensions such as valence or arousal, classifying emotions into specific categories of individual emotions requires more inference and generally involves cortical sensory regions in addition to subcortical structures. The cortical regions involved are generally those that represent that sensory modality and its specialized processing aspects. For instance, categorizing emotion from facial expressions involves cortical regions in the temporal lobe known to represent faces or biological motion; categorizing emotion from voices involves primary and higher-order auditory cortices. MVPA has shown that there is information about emotion categories in the activation pattern seen in face-selective areas of fusiform gyrus [37], the medial prefrontal cortex [28] (to which we return below), and the superior temporal sulcus [48] (involved in face and biological motion processing). Yet it is important to note that strong evidence

for fine-grained representation of different emotions is still lacking, in good part because most studies only contrast one or two emotions, but not a large number of emotions.

Related to difficulties in investigating representations for specific emotions are two further important points. First, one might think that the sparse sampling of different emotions in any single neuroimaging study could be overcome simply by *meta*-analyses that look across a large number of studies. This has in fact been done in a number of *meta*-analyses, which conclude either that there is no specificity in how the brain represents individual emotions at all [25], that such representation is overlapping and distributed [47], or that it is lower-dimensional than for specific emotions (e.g., just for valence, as supported also by some individual research studies; [6]. One problem with all these is that the studies going into the *meta*-analyses are of mixed quality and highly variable in stimuli and tasks, making it difficult to extract specific conclusions. Another problem is that the resolution of fMRI, especially univariate fMRI, may well be too low to resolve representations of distinct emotions. Indeed, as we saw above, the best emerging evidence for specific emotion representations comes from MVPA, not from univariate analyses.

But a second important problem for investigating the neural basis of recognizing specific emotions is to decide what those emotions should be in the first place. There is a commonly used set of about six "basic" emotions (happiness, surprise, fear, anger, disgust and sadness), which are the set that psychologists like Paul Ekman have claimed are recognized universally across cultures [9]. But there is also good emerging evidence that in fact emotions are not categorized similarly across all cultures at all (from either face or voice; [13,14] making it unclear what should be the "ground truth" for how to divide up the categories. Even if there were consensus on the categories to include, issues remain with the common practice of using prototypic, exaggerated facial expressions to represent them. This is because people rarely encounter the prototypic form of some emotions, such as fear [38]. In addition to introducing problematic confounds in prior experience between emotion categories, such a lack of realism in the stimuli used in these studies imposes strong limits on the ecological validity of the psychological processes being elicited [50].

Following a historical proposal by William James [20], several modern theories of the conscious experience of emotion (feelings) hypothesize that we feel emotions in virtue of our brain representing the body states associated with the emotion [8,7]. In light of studies showing that observers often mimic (i.e., mirror) the emotional behavior of others, James' mechanism suggests that observers may understand *what* others are feeling because they can vicariously experience the same feeling in themselves i.e., that we *simulate* the body state of another person by representing that state in somatosensory-related regions (S1, S2, insula) in our own brain [17]. In support of this hypothesis, lesions of somatosensory-related cortices (particularly in the right hemisphere) disrupt people's ability to recognize facial emotion [2]. Most interestingly, fMRI studies have found that MVPA of regions within right somatosensory cortex represented information about specific facial expressions, and that this representation showed some somatotopy such that specific emotions could be decoded from those regions of S1 that represent the facial features most diagnostic for that emotion (such as wide eyes for fear; [23].

4. Why are they feeling it? Causal attribution of emotion

Imagine witnessing your close colleague pound their fists while seated at their desk, mouth agape as they glare at their computer monitor. To fully understand this emotional situation, it would be insufficient to merely recognize that your colleague is angry. Instead, observers need to generate a coherent account, an explanation, of what it is that they observe: they need also to understand *why* the other person feels the way they do, and this is accomplished by making causal attributions. This final, richest, aspect of emotion understanding thus involves two components that each map onto somewhat distinct neural regions: (1) an understanding of the emotion in terms of semantic knowledge about the emotion (often encoded in language); (2) an understanding of the emotion in terms of its causes. The first involves brain regions that store semantic conceptual knowledge; and the second brain regions broadly involved in Theory of Mind (Fig. 2).

For component (1), regions within the anterior temporal lobe (ATL) are believed to be critically involved in maintaining conceptual knowledge about the social world. Such knowledge includes

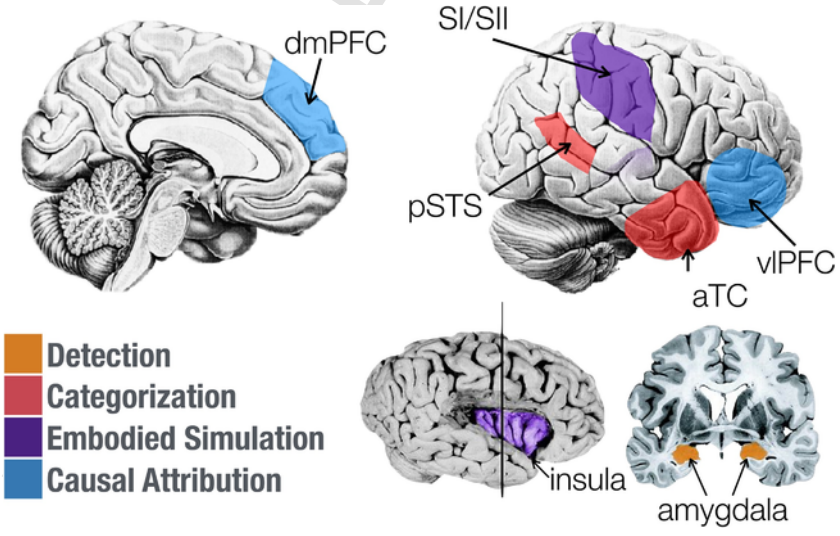

Fig. 2. Selected brain structures implicated in the different functional components of emotion understanding discussed in the main text. Each structure is color-coded to indicate, based on existing evidence, the component(s) to which it contributes. To enable a clear visualization, a number of structures known to be involved in emotion understanding are discussed in the main text but not shown in this figure. aTC, anterior temporal cortex; pSTS, posterior superior temporal sulcus; dmPFC, dorsomedial prefrontal cortex; vlPFC, ventrolateral prefrontal cortex. Portions of this figure adapted from [1].

both specific facts about familiar others (e.g., their first name, favorite foods) [44,19], as well as more general abstract beliefs about the world, such as place-specific behavioral norms and mental-state and trait concepts [49,24].

For component (2), the attribution of identified emotions to abstract causes is likely supported by regions in the dorsomedial and ventrolateral prefrontal cortices. These regions are thought to implement executive functions for retrieving relevant abstract knowledge and selecting among competing interpretations of complex stimuli [33,10,16,18], functions that, in the domain of emotional and social inference, typically take the form of mental-state inferences [40,41,37,22,36]. Indeed, *meta*-analyses of neuroimaging studies of theory-of-mind reasoning in its various forms reliably implicate these same regions [46,4,11], and the specific association with tasks used to assess theory-of-mind is particularly reliable for the dmPFC [35].

5. Outstanding issues

By way of conclusion, we briefly identify several questions and issues that would be important to tackle in future neuroscience research on emotion understanding. Two general issues that face current studies are about details: to provide a more detailed account of the different processes schematized in Fig. 1 and to understand how they interact; and to provide a more detailed, and possibly different, set of emotion categories. Addressing both of these issues will require careful attention to task design, and will likely require obtaining behavioral performance measures as well as experimental designs informed by computational models. It will also require a close consideration of individual differences (e.g., goals, beliefs, prior experience) that might lead different observers to different interpretations of an emotional stimulus (e.g., [39].

Another rich domain will be to understand the automatic or controlled nature of emotion understanding (for further discussion, see [42]. While we believe that both processing aspects are involved, the assumption has generally been that emotion inference is relatively automatic. Can we control how we see emotions in other people? If so, can we train people to see others differently? These important open questions are also relevant for disorders such as autism, in which emotion inference is atypical.

A final topic for the future would be to bring the investigation of self-attribution of emotions closer to the literature we have reviewed here. Do we engage some of the same neural systems when we attribute an emotion to ourselves as we do when we attribute emotions to others? While self-relevant processing has also prominently highlighted one of the nodes we noted above—the dorsomedial PFC—it remains quite opaque what to put into the bottom two levels of processing in Fig. 1, since we do not know what normally starts an emotion understanding process when it is applied to oneself.

Acknowledgment

Funded in part by NIMH grant 2P50MH094258.

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