Advanced Review

Neural basis of affect and emotion

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Research on affect and emotion has recently been informed by novel methods and theories in cognitive neuroscience. This perspective, known as affective neuroscience, has the potential to dramatically improve our understanding of fundamental processes of emotion. In this article, we review the major neural systems involved in emotion and consider the computational properties of these regions. Specifically, we consider affect systems associated with the representation of predicted and experienced affective states, the cortical re-representation of body states, and the role of reflection in generating and maintaining emotional episodes.

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INTRODUCTION

One of the most exciting developments in modern psychology has been the recent application of the theories and methods of cognitive neuroscience to the study of psychological phenomena. Although this technology has provided new insights into nearly all aspects of psychology, ranging from visual perception to complex decision making, the study of affect and emotion from a neuroscience perspective has been particularly fruitful.[1–3] For much of the 20th century, mainstream experimental psychology had difficulty answering questions about the structure and function of emotion, in part because emotions were considered to be in the realm of subjective experience and not reducible to more fundamental cognitive processes.[4,5] With the development of increasingly sophisticated techniques for detecting changes in the body and imaging the brain, an emerging field, affective neuroscience, has generated renewed enthusiasm with its promise to transform the study of emotion.[6–8]

In this article, we review our current understanding of the major neural networks associated with affective processing and suggest the ways in which these networks might interact to create emergent emotional structure. For the purposes of this article, we define *affect* as a feeling of positivity or negativity (i.e., pleasure or displeasure) with some degree of intensity or arousal, and *emotion* as a more distinctive set of behavioral, cognitive, and physiological responses. In other words, we consider affect as a necessary but not sufficient component of emotion. After reviewing the existing literature, we propose a framework based on the iterative reprocessing model[9] for understanding emotion as constructed from a series of increasingly complex iterations of neural activation of affective information through time.

THE FUNCTIONAL ROLE OF AFFECT

For thousands of years, at least in Western civilization, the concept of emotion has been considered the antithesis of reason.[10] For this hydraulic model, emotions are considered to be the remnants of our ancient animal nature (i.e., our reptilian brain) that take control of our thoughts and behaviors, making us susceptible to environmental influences and removing personal agency. From this view, any emotion necessarily clouds reason and must lead to suboptimal decisions. However, empirical data suggest that the idea that emotions always led us astray is not accurate. For example, one of the first affective neuroscience case studies involved Phineas Gage, a railroad foreman who had large areas of his medial prefrontal cortex (PFC) damaged by an iron rod. Interestingly, although his logical thinking abilities remained largely intact, he was no longer able to integrate emotional information into his decision-making processes and as a result, his ability to function within society was dramatically impaired.[11] Neuropsychological studies over the past century have found similar patterns and demonstrated that patients who have damage to the orbitofrontal cortex (OFC) and/or amygdala (regions thought to be critical for emotion) are typically unable to integrate affective cues into their behavior and as a result have impaired decision-making skills.[12–14] Rather

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than being detrimental to reason, affect provides information about what is important to us, indicates how events are likely to affect us, and allows for an ability to plan for the future through simulation of future consequences of behavior or other potential outcomes. Thus, emotions are intrinsically neither good nor bad, but rather provide information about the environment and the place of the person in the environment that can be used to facilitate planning and decision making.

NEURAL BASIS OF AFFECT

Typically, affect is defined as a set of dimensions encompassing valence (positive or negative) with some degree of intensity or arousal.[15–18] On the surface, this definition should allow for a relatively straightforward mapping between the psychological affect concepts (e.g., valence) and brain function. However, when evaluating existing knowledge about the neural architecture of affect, we find that the relationship between these dimensions and brain activity is not so simple.[7,9] Critically, affect appears to be re-represented at multiple levels of the neuroaxis, with increasing flexibility of affective responses as one moves from the spinal cord to the brain stem, limbic system, and then cortex.[19] Indeed, even within the OFC, affective information appears to become more abstract as one moves from posterior to anterior regions.[20] Thus, to fully understand the neuroscience of affect, one needs to move beyond a relatively simple valence/arousal distinction and begin to articulate the specific contributions of various neural systems to the generation of an emergent affective (or emotional) state.

Some understanding of the fundamental computations involved in affect can be gained by looking at other systems that are psychologically similar. For example, affect shares a basic resemblance to how we learn via reinforcement: both systems involve anticipation or prediction of positive and negative outcomes as well as receipt of those outcomes. Indeed, the neural systems involved in affect and emotion share considerable overlap with the systems involved in reinforcement learning.[21–26] For example, both systems involve processing the prediction and receipt of positive and negative consequences, and updating behavior accordingly. But although reinforcement learning and emotional processing share a number of neural regions and processes, they also have unique properties and functions. For example, affect typically also includes a body response that is integrated into ongoing subjective experience. In addition, many models of emotion suggest that some degree of cognitive appraisal is necessary to translate (and retranslate) these affective states into an emotion category.

Given the functional role of affect in successfully navigating one's environment, we seek to understand the major corresponding regions and their interactions. Together, these regions represent our current affective state as a function of affective movement through time, integration of bodily feedback, and organization of thoughts and behavior. Importantly, emotional processing can begin anywhere in the system, as sometimes a stimulus may only be recognized as relevant to one's affective state once a certain amount of evaluative processing has taken place. Multiple connections among brain regions also allow for cross-system communication.

PREDICTING FUTURE AFFECTIVE STATES

An affective response typically follows a perception of a self-relevant stimulus.[27] We feel threatened when we are stopped by a police officer or excited when we see our favorite dessert at the local sweet shop. Although we can define these two experiences as simply negative and positive valence, respectively, they represent a particular type of valenced representation—one that involves the anticipation of a future affective state. That is, when we see the flashing lights in the rear view mirror, we imagine that something unpleasant is about to happen (getting a ticket, being late to work, or worse) and when we see the cheesecake, we imagine soon having a positive gustatory experience (and maybe a little evolutionary desire for calories will be satisfied). What is critical in these examples is that the negative or positive experiences have not yet happened, but instead are simulated by the mind using our previous experience as a guide.[8]

When considering the regions involved in the learning and use of evaluative information for prediction, the amygdala has received the most attention. Although initial work suggested that the amygdala might be primarily involved in threat detection and the processing of negative stimuli,[28–31] recent work has found that it is also sensitive to positive information.[32–34] The ability of the amygdala to represent both positive and negative valences may indicate that the amygdala response is independent of valence, perhaps representing the arousal value or intensity of the stimulus,[35,36] although recent research in monkeys suggests that these responses may instead represent separate populations of neurons with the amygdala that are differentially tuned to positive or negative information.[37] The valenced information that the amygdala is most responsive to can also vary as a function of a person's chronic[38,39] and situational goals.[40] Specifically, the amygdala is more responsive to appetitive stimuli when positive information is most important in a given context, while it is more responsive to aversive stimuli when negative information is most important. Thus, the amygdala seems to be tuned to respond according to whatever is most appropriate or salient at that time.

An examination of the anatomic connections with the amygdala suggests that this region is well suited for automatic vigilance and organized response functions.[41] Specifically, the amygdala is well connected with widespread areas associated with perceptual processing and autonomic activation.[42,43] Thus, following amygdala activation, greater attention can be directed to the stimulus while the body prepares for action. The amygdala is also multiply connected with areas involved in more deliberate forms of decision making, such as areas of orbitofrontal, insular, and lateral PFC.[44,45] Through its wide network of reciprocal connections, information processed in the amygdala can be integrated through sensory, motor, and cognitive processes and modulated to take into consideration the entire state of the individual. Thus, following amygdala activation, the opportunity is present for multiple brain systems to dynamically reorganize to appropriately deal with the current environment.

One critical proposed aspect of amygdala function relates to how it can evaluate the rapid stream of incoming information. Current research supports the idea that it operates relatively automatically and unconsciously. For example, conscious awareness of a valenced stimulus does not appear to be necessary to produce amygdala activation. In a conceptual replication of previous research on supraliminal face processing,[30] it was demonstrated that subliminal presentations of fearful faces led to amygdala activation.[46] Another set of studies found that after participants were classically conditioned to associate particular angry faces with an aversive stimulus, the amygdala showed greater activity to these conditioned faces than to the control faces, using both subliminal and supraliminal presentations.[47] A third set of studies used depth electrodes in individual cells of the amygdala to demonstrate that processing of valence (i.e., greater neural firing to valenced as opposed to neutral stimuli) occurs just 200 ms after stimulus presentation.[48] Taken together, this work indicates that the human amygdala responds rapidly to valenced stimuli, even when people are not consciously aware of those stimuli.

Although much scientific attention has been directed toward the amygdala, evaluative processes are associated with a much larger circuit involving additional cortical and subcortical regions. Among the more critical subcortical regions associated with evaluation is the ventral striatum, and more specifically the nucleus accumbens (NAcc). Linking NAcc activity to evaluation, studies on economic decision making suggest that NAcc activity is not only correlated with, but may even be a better predictor of a participant's choice to buy a particular product than self-report[23] (but also see Ref 49). Critically, although amygdala activation appears to be associated with the evaluation of both positive and negative stimuli, the NAcc is primarily involved in the anticipation and/or receipt of incentives or rewards.[23,50,51]

REPRESENTING CURRENT AFFECTIVE STATES

Although activity in the amygdala and NAcc has been shown to play a role in predicting the consequences of a stimulus, directing attention toward affectively significant stimuli, and automatically preparing for behavior, these patterns of activation do not necessarily predict one's current subjective affective state. Instead, information regarding expected outcomes is passed from limbic areas to the OFC, where it is evaluated with respect to current well-being, for example, through attainment of one's goals. In other words, while the amygdala and NAcc provide information regarding predicted outcomes following the perception of a stimulus, OFC represents the current (or anticipated) affective experience as a result of those outcomes. Specifically, the OFC is responsible for the subjective pleasure associated with receiving (or displeasure associated with not receiving) an expected outcome or the anticipation of a likely outcome.[52] Just as there is evidence in the prediction circuits for dissociation in processing of positive and negative information, there is some suggestion that different areas of the OFC are sensitive to different types of outcome-related information. Specifically, activity in medial OFC is typically related to evaluations of positive or rewarding information, whereas activity in lateral OFC is related to evaluations of negative or punishing information.[35,53,54]

Because OFC receives input from multiple sensory modalities, it may provide a common metric for representing and comparing different aspects of evaluative information,[26,55–57] including the evaluative connotations of self-generated mental representations.[58] Activity is evident in response to primary rewards such as food or drink[26,52] as well as secondary or symbolic rewards such as money.[59–61]

OFC activity has also been linked to the evaluation of the relative appropriateness of one's responses, activating both to receiving rewards and avoiding punishments.[20,62] Thus, although the ways that we subjectively consider the evaluative connotations of a friendship, a new car, or the ideals of egalitarianism appear vastly different, they can be reduced to a common evaluative dimension and directly compared.

To the extent that the amygdala and NAcc provide a low-resolution estimate of expected outcomes following the perception of a stimulus and the OFC represents the current state of the organism, the dense reciprocal connections between amygdala and OFC allow for a comparison of expected rewards and punishments with current experience. This idea is supported by research demonstrating increased activity in the OFC following violations of expectancies[63] and the inability of patients with OFC damage to update current representations when predictions and outcomes are incongruent.[64,65] Certain regions of the OFC are likely to be involved with not only representing our current state, but also integrating the current state with output from the amygdala to compare expected rewards or punishments with current experience. This allows context to play a role in shaping our affective response.[14,26,66,67] Because the OFC can represent anticipated outcomes, actual outcomes, and the comparisons between these representations, this region is likely critically involved in the generation of emotional states that require affective information to be compared and contrasted across time.[68] In other words, the current state is a composite of our momentary affective standing based on comparisons with other points in time.

GENERATING AND INTEGRATING BODILY RESPONSES

Autonomic feedback is considered by many perspectives to be a key feature of emotional experience, even sometimes the essence of emotion itself.[69] For example, Barrett and Bliss-Moreau[70] suggest that sensory information from the world is represented in somatovisceral, kinesthetic, proprioceptive, and neurochemical fluctuations and that these bodily representations form a 'core' affective state. This body state is cortically re-represented in the somatosensory cortex, particularly the insula, which can then be integrated into subsequent steps of affective processing through connections to the amygdala and OFC.[8,12,26,71] Cortical interpretations of these body states can provide information about the state of the individual and, following some cognitive interpretation, lead to the development of more nuanced emotional experiences (see section on *The Reflective Processing of Affective Information*).

In addition to using information from the body to inform brain states, changes in affectively related brain states often lead to changes in body states. For example, once a potential threat has been detected, the body may need to organize in preparation for an immediate fight or flight response.[72] When a relevant stimulus is encountered, information about the stimulus triggers an immediate motivational tendency to approach or avoid it, producing a series of reflexive reactions that prepare the body for immediate action. Importantly, dense connections exist among each of the regions previously discussed (i.e., amygdala, NAcc, insula, and OFC) such that changes in one region can be represented in each of the others. Furthermore, these regions project to the hypothalamus, which sends information to a variety of structures involved in coordinated motor, endocrine, and neuromodulatory responses.[5,73]

THE REFLECTIVE PROCESSING OF AFFECTIVE INFORMATION

Although affective responses begin with some combination of physiological activation and neural evaluations, emotional episodes also appear to involve some degree of cognitive interpretation.[15,74] That is, although we can represent affective predictions and body states cortically, some degree of meaning may need to be attached to these feelings to generate familiar emotions such as fear, anger, sadness, or joy. According to these models, we can translate undifferentiated physiological sensations that have no particular emotional meaning by considering the situation in which they occur. For example, we can define the same increasing pulse rate as fear, anger, or even infatuation or love by attending to different features of the environment.[75–78] Thus, experiencing a separate or discrete emotion may reflect a process of categorizing continuous affective experience using a discrete label that is then used as an interpretive framework.[15,17,79] Similarly, appraisal models suggest that emotion reflects a cognitive interpretation of the overall current state of the system.[80–82] That is, our appraisals about affect—such as who or what is causing it, how much control we have, whether the state is consistent with our goals, and so forth—help to understand and even define our emotional experience. The particular emotion that is experienced may be largely dependent on the aspects of the situation or object to which one attends.[83,84] The situation reflects the perceiver's unique interpretation of his or her surroundings in terms of personal relevance.[6]

The corresponding neuroscience research supports this approach: our initial affective responses may be simple, rough, and automatic, consisting largely of information about valence, whether the trigger has personal significance, and relatively simple approach or avoidance responses. However, as more processing of the information occurs, additional prefrontal resources can be recruited to help produce a more nuanced or developed emotional response.[9] For example, while walking to one's car late at night, a light breeze could cause a shiver (affect originating from the body) or a shadowy figure may be seen from the corner of one's eye (affect originating from a prediction). Following these changes to affect, one becomes attentive to situation, noticing the disrepair of the surrounding buildings and their darkened alleys. This additional semantic detail can be integrated with the affective signals to appraise the situation (threatening), label one's feelings (fear), and then use this information to determine an appropriate course of action (run to the car!). Consistent with this idea, participants who read negatively valenced sentences before viewing surprised faces had greater amygdala activation relative to positively cued faces, demonstrating that the context in which the faces were viewed was important in modulating the amygdala response.[85] This type of processing does not necessarily generate a completely new affective state, such as changing one's negativity to positivity, but can modulate activity in lower-order regions[35,86,87] and help to generate a unified response. In other words, through cognitive processing and attaching meaning to affective states, an emergent emotional state can be generated and maintained by activating particular prototype-consistent interpretations and activating stereotyped behavioral responses.[15,17,88]

In addition to defining our initial emotional experiences, similar processes can be used to change our affective or emotional responses. Just as appraisal can attach meaning to an affective event, reappraisal can change this interpretation and subsequently modify the experience of that emotion.[89] In the above example, after contemplating the possibility of danger, one might assess resources at one's disposal to cope with the situation, such as martial arts training or pepper spray, and as a result start to feel confident rather than afraid. Consistent with this hypothesis, when participants are asked to reappraise negative images as positive (e.g., seeing a sick man as not ill, but getting better), greater lateral PFC activity and decreased amygdala activity are observed.[86] Furthermore, reappraisal does not necessarily need to lead to a decrease in affective processing. In a follow-up study, participants were asked to either upregulate (make themselves feel more emotional) or downregulate (make themselves feel less emotional) their affective responses to pictures. The same area of lateral PFC was associated with both increasing and decreasing the amygdala response.[87,90]

CHALLENGES AND PROMISES

Until relatively recently, emotions were thought to represent activation of specific biological modules corresponding to a small set of discrete emotions (e.g., happiness, sadness, fear, and anger).[91–93] Once an emotion module was activated, a stereotyped set of responses would follow, including changes in physiology, facial expression, behavior, and subjective experience. However, over the past half century, little evidence has been found to support distinctive physiological signals of emotion[94] or distinct brain patterns associated with specific emotions.[95–97] Partially for this reason, researchers have begun to consider alternative models to explain emotion processes. For example, the psychological constructivist perspective[6] suggests that we have a limited number of basic mental ingredients that can be combined in various ways to produce a number of different experiences, including emotions, thoughts, memories, and so forth. Although there are some fundamental, irreducible components to our mental life, they are flexible and multifunctional. Thus, emotions can be likened to a set of recipes: the mental ingredients that form these recipes can combine in varying ways to produce different emotions.

On the basis of the neuroscientific literature reviewed above, our laboratory has developed a framework to understand how specific emotions (e.g., fear, anger, sadness, and hope) can emerge from this hierarchical cognitive system.[68] This approach allows for the generation of discrete emotional states while conforming to current beliefs about the cognitive and neural architecture of the human mind. Consistent with the review above, we propose that individuals maintain representations of valence at any given moment that can be used to determine an affective or emotional state. *Previous* affective states are composed of memory representations of an individual's immediate affective past. The *current* affective state is an evaluation of one's current state as a function of outcomes. *Predicted* affective states are an evaluation of what is likely to happen next. Current affective state is conceptually similar to the idea of core affect (though representing a cortical common currency rather than a body state), and the predicted hedonic state is similar to anticipated affect.[17] Critically, comparisons can be made between these time points through communication among the relevant neural circuits, allowing us to map out our particular affective place in time. In making these comparisons, we are particularly sensitive to changes in valence, such as when a positive state worsens over time. Patterns of interaction between current state, predictions, and outcomes can lead to the perception and labeling of specific emotional states. At each stage of the process, what was the current affective stage becomes the previous affective state, and new predictions are generated (Figure 1). Yet, although emotions are generated through a dynamic cycle of processing, some emotions may result from attention to only parts of the system. For example, the emotion category fear may simply require labeling the feeling state generated by a negative prediction signal. Others, such as joy or sadness, may require more comparison; for these examples, this comparison might reveal an upward or downward affective trajectory, respectively.[98] In contrast to models that tacitly begin emotional processing after stimulus presentation (at a figurative 'time zero'), this perspective suggests that emotional states are rarely separate from the affective and motivational context in which they arise and may, in fact, necessarily require changes in affective processing from previous to current states.[9]

This approach suggests that the current paradigms we employ for studying emotion may not be the most effective for capturing emotional processes. Many functional magnetic resonance imaging (fMRI) studies induce emotions by showing participants stimuli such as a picture of a fearful facial expression, a negatively valenced film clip, a person with an aggressive stance, and so forth. Moreover, studies typically show participants stimuli from multiple emotion categories in rapid succession (e.g., faces that display fearful, then happy, then disgusted expressions). Although such studies may be ideal for identifying some general affective aspects of processing, they may be less well suited for examining emotional episodes. Emotions may need to be understood as emerging from more dynamic contexts than those typically manipulated in neuroimaging studies. In other words, one reason that we may have failed to find unique neural signatures of emotions may stem from the fact that we have not manipulated the appropriate components or 'ingredients' that build an emotional episode. With this in mind, we suggest that future emotion research may benefit from articulating the ingredients of emotion and manipulating these individually to more organically create an emotional episode during a scanning session.

CONCLUSION

Neuroscience methodologies and perspectives have been useful tools in the continuing process of understanding how affect manifests in the human brain, and the implications of these findings for models of emotion. Much is now known about the neural systems involved in affective processing that was relatively inaccessible even 20 years ago. In our review of the literature, we identify four aspects of affective processing. These include the generation of affective predictions for the future, the representation of current affective states, the integration of information from the body, and the engagement of reflective processing

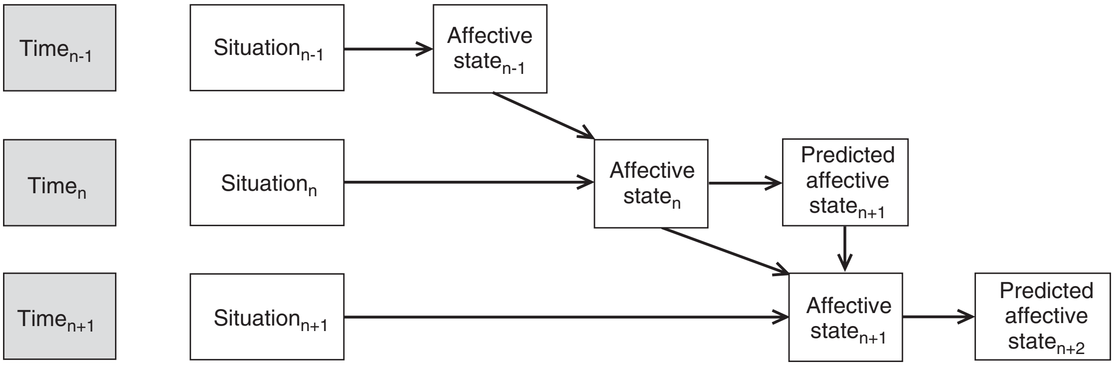

FIGURE 1 | Multiple determinants of emotional state. At any given moment in time, an individual's current affective state is partially determined by (1) the situation, or what is occurring in the environment and (2) the individual's affective trajectory: comparing the current state of the world with what the individual had predicted for himself. A current affective state also naturally leads to a prediction for the future: whether things will improve, worsen, or remain the same. For example at Time $[n+1]$, the individual's affective state is jointly determined by his representation of the world at Time $[n+1]$ and what he had predicted for himself at Time $[n]$. This composite affective state informs a prediction for his affective state at Time $[n+2]$.

to integrate appraisals, interpretation, categorization, and meaning. When taken together, these four aspects of affective processing may result in the experience of discrete emotional states. Future work is needed to more directly explore the integration of these processes.

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