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The Information Processing Role of the Amygdala in Emotion

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1. Introduction

The term "emotion" usually refers to brief and intense affective feelings. Numerous philosophers and writers have noted since ancient times that emotion greatly influences our lives. Thus, researchers and laypersons both are very interested in emotion. Recently, neuroscientific studies exploring the neural substrate for emotion have suggested the involvement of the amygdala in emotion, but its specific role remains unclear.
This article reviews previous research and attempts to summarize how the amygdala processes information on emotion. First, I discuss emotion as a series of information processes based on evidence from the psychological literature. Then, I present compiled anatomical information on the amygdala and give evidence for the involvement of the amygdala in emotion. Finally, I explain the general framework and details about how the amygdala processes information on emotion.

2. Psychological discussion on emotion

Emotion is a subject in psychology that also draws the attention of non-psychologists, but a large difference exists between the popular concept and psychological perspectives of emotion. Popularly, people tend to emphasize the subjective aspects of emotion (Cornelius, 1996) and sometimes wonder whether emotion is too personal to be a subject of scientific research. Psychological research provides a different perspective on emotion, and although summarizing the psychological research on emotion is difficult because it is extremely varied, I believe that three findings are important for the study of emotion when we discuss the relationship to its neural mechanisms.
First, emotion clearly includes widespread responses. For example, some research on expressions has indicated that emotions induce specific expressive behaviors. Ekman et al. (e.g., Ekman & Friesen, 1975) found that people commonly display specific facial expressions when they feel specific basic emotions (e.g., anger). In addition, emotion generates physiological responses. Some studies measuring autonomic nervous activity have shown that each type of emotion generates a specific physiological response pattern (Levenson, 1991). Moreover, emotion modulates cognitive activities, including perception (Öhman et al., 2001) and memory (Bradley et al., 1992). Studies that recorded multiple measures simultaneously indicated that the subjective, physiological, behavioral, and cognitive responses of emotion are intimately related (Lang et al., 1998).

Second, emotion is proposed to be an adaptive function of the mind acquired in the evolutionary process (e.g., Tooby & Cosmides, 1990). Darwin (1872/1998) first analyzed emotion from an evolutionary perspective and provided some evidence to support his idea. Subsequent Darwinist researchers systematically gathered evidence of inter- and intra-species universalities for emotional expressions, which strongly suggested that human emotion was acquired evolutionarily (Ekman, 1999). From the perspective of evolutionary functionalism, emotion can be viewed as a biological function designed for adaptation, promoting the survival and reproduction of individuals in response to the environment. Emotion still has an adaptive function that may partially reflect past environments (Keltner & Gross, 1999).

Third, researchers pointed out that before an emotional response is produced, one conducts a process of appraisal (e.g., Arnold, 1960). Indeed, for the identical stimulus, the emotional responses can differ from individual to individual. In addition, the emotional response of an individual can differ depending on the context. Before producing an emotional response, the appraisal mechanism must assess the relevance of the stimulus in terms of the current state of the individual. Many researchers (e.g., Arnold, 1960) have posited that the appraisal process in emotion is not necessarily intentional, but is automatic and sometimes cannot be accessed subjectively. Although the nature of appraisal in emotion remains inconclusive, most researchers appear to agree that emotion involves an appraisal process.

Taken together, emotion, as discussed in the psychological literature, is a series of information processes that appraise the adaptive significance of stimuli and generate various adaptive responses accordingly (Fig. 1).

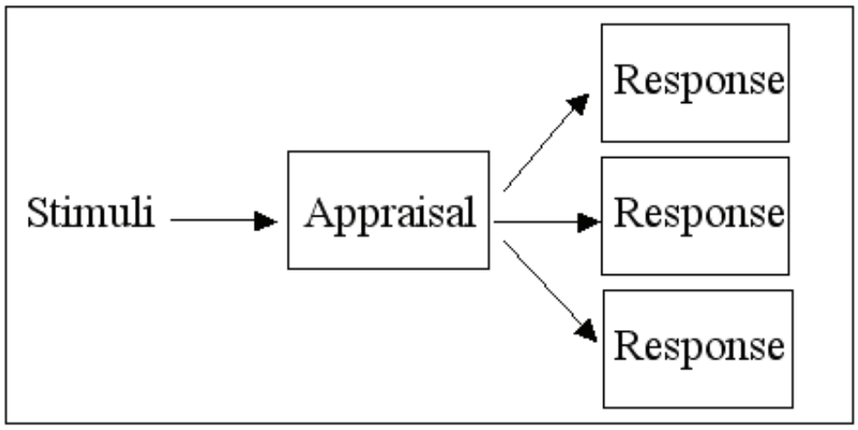


Fig.1. Emotion as a series of information processes.

Emotion is regarded as a series of information processes that evaluate the adaptive significance of stimuli and produce distributed adaptive responses accordingly.

3. Anatomy of the amygdala

The anatomy of the brain sets important constraints on and provides clues to cognitive functions. Hence, I will briefly summarize the anatomy of the amygdala. The amygdala is an almond-shaped mass of gray matter located bilaterally within the anteromedial part of the temporal cortex. The volume of the amygdala on one side is about 1700 mm^3 based on the overall mean across studies (Brierley et al., 2002).

Although it is a small organ, the amygdala has a complicated internal structure comprising a complex of nerve nuclei. Anatomical studies in monkeys suggest that it consists of 13 distinct nuclei (Amaral, 2002) that form an intricate neural network (Aggelton & Saunders, 2000), including multistage serial processing pathways that process sensory signals. For example, the visual signals are input from the temporal cortex to the lateral nucleus, which projects them onto the basal nucleus; the basal nucleus then projects them onto the central and medial nuclei. In addition, parallel processing pathways are involved, for example, the lateral nucleus projects on the accessory basal nucleus, as well as the basal nucleus.

Anatomical studies in monkeys have revealed intriguing relationships between the amygdala and other brain regions. As inputs, the amygdala receives projections from one or more sensory regions representing each sensory modality (Amaral et al., 1992), which suggests that the amygdala can process sensory stimuli of all modalities. Concerning the visual and auditory modalities, input projections travel via both subcortical and cortical structures. For example, while the optic pathway goes through the primary visual cortex in the occipital lobe, bypassing projection pathways to the amygdala are routed via the superior colliculus and pulvinar, enabling the rapid processing of sensory information. As outputs, the amygdala has dense projections to many brain regions that are important in implementing various types of bodily and cognitive responses, including the brain stem, hypothalamus, hippocampus, basal ganglion, and cortical regions (Amaral et al., 1992).

In summary, the amygdala is a neural region that has a complex inner structure, receiving input from all sensory modalities and sending output to various brain regions.

4. Evidence for involvement of the amygdala in emotion

Lesions studies in monkeys provide clear evidence that the amygdala is involved in emotion. A seminal study by Kluver and Bucy (1939) reported dramatic changes in the emotional behaviors of monkeys after lesioning the anterior temporal cortex, which included the amygdala. For example, the lesioned monkeys approached snakes, which normal monkeys fear. Subsequent studies showed that the impaired emotional behavior was caused by selective lesions of the amygdala. For example, Amaral et al. (2003) examined the effect of selective amygdala damage in monkeys. The monkeys with damaged amygdala did not show fear in response to threatening environmental stimuli, such as snakes. In addition, when the lesioned monkeys were put in a cage with unfamiliar individuals—a situation in which normal monkeys become nervous and aggressive - the subjects did not show any emotional arousal.

Human studies also provide evidence of the involvement of the amygdala in emotion. For example, a neuropsychological study reported that a patient with bilateral amygdala damage showed the loss of subjective and behavioral responses involving certain negative emotions (Tranel et al., 2006). Electric stimulation studies in epileptic patients have revealed that stimulation of the amygdala sometimes induced subjective experiences and the facial expressions of fear (Gloor, 1997). A functional neuroimaging study (Breiter et al., 1996) measured the brain activities in normal participants using functional magnetic resonance imaging (fMRI) while observing facial expressions showing fear, happy, and neutral emotions. Emotional facial expressions of others have been shown to induce contagious emotional responses in observers (e.g., Johnsen et al., 1995). The amygdala was more active in response to fearful and happy facial expressions than to neutral expressions.

In summary, these findings demonstrate that the amygdala is indeed involved in emotion.

5. Information processing related to emotion in the amygdala

What information does the amygdala process regarding emotion?
Electrophysiological studies in animals have shown that the amygdala neuron activity in response to external stimuli reflects the adaptive significance of stimuli and not their sensory characteristics. For example, Ono and Nishijo (1992) conducted single unit recordings in a monkey and investigated the amygdala activity in response to visual stimuli. First, they identified the amygdala neurons that responded to the sight of food, such as an orange. Then, they salted the food and made the monkey taste it. As a result, the amygdala activity in response to the sight of an orange disappeared immediately. When the researchers gave unsalted food to the monkey, the responses of the amygdala neurons to the sight of food recovered quickly. Note that the salted food looked the same as normal food, but differed in its adaptive significance. These results suggest that the amygdala is not engaged in the basic sensory analysis of environmental stimuli, but in appraising their significance.
Lesion studies in monkeys and rats have also indicated that selective damage to the amygdala impairs the triggering of emotional responses to emotionally significant stimuli (Aggleton & Young, 2000). For example, a series of experiments in rats by LeDoux and his colleagues (LeDoux, 1998) indicated that the freezing response to fearful stimuli disappears after destroying the central nucleus of the amygdala, which projects to the central gray matter in the brain stem. The amygdala, however, is not involved in the response itself. In this case, even when the amygdala was destroyed, the freezing response could be elicited by electric stimulation of the central gray matter. Therefore, the production of the emotional response "freezing" should be regarded as relating to the central gray matter directly. The amygdala likely generates commands for other brain regions regarding appropriate responses that are based on appraisals of their significance.
In line with these animal data, human neuroimaging studies have demonstrated that amygdala activity corresponds to the emotional significance of stimuli and emotional responses. For example, an fMRI study (Sato et al., 2004) examined this issue using the interaction between facial expressions and face directions (Fig. 2). Angry and neutral expressions looking toward and away from participants were presented in unilateral visual fields. The emotional significance of the angry expressions differed markedly between face directions, although the physical features of the stimuli were comparable. After acquiring the image, the participants' experience of negative emotion for the stimuli was also investigated. The study yielded two main results. First, the amygdala showed an interaction between emotional expression and face direction, with greater activity for angry expressions looking toward the subjects than angry expressions looking away from them. Second, the amygdala activity showed a positive relationship with the emotion experienced. The first result matches the idea that the amygdala is involved in appraising significance after the basic sensory processing of stimuli. The second result supports the idea that the amygdala is related to the emotional response.
Combined, the animal and human data suggest that the amygdala is involved in multiple processes that first evaluate the adaptive significance of stimuli and then generate commands for other brain regions regarding adaptive responses (Fig. 3). This concurs with the hardware characteristics of the amygdala. As the amygdala has a complex inner structure and receives all sensory inputs, it is well equipped to evaluate environmental stimuli. In addition, the amygdala sends output to several regions that are related to emotional responses.

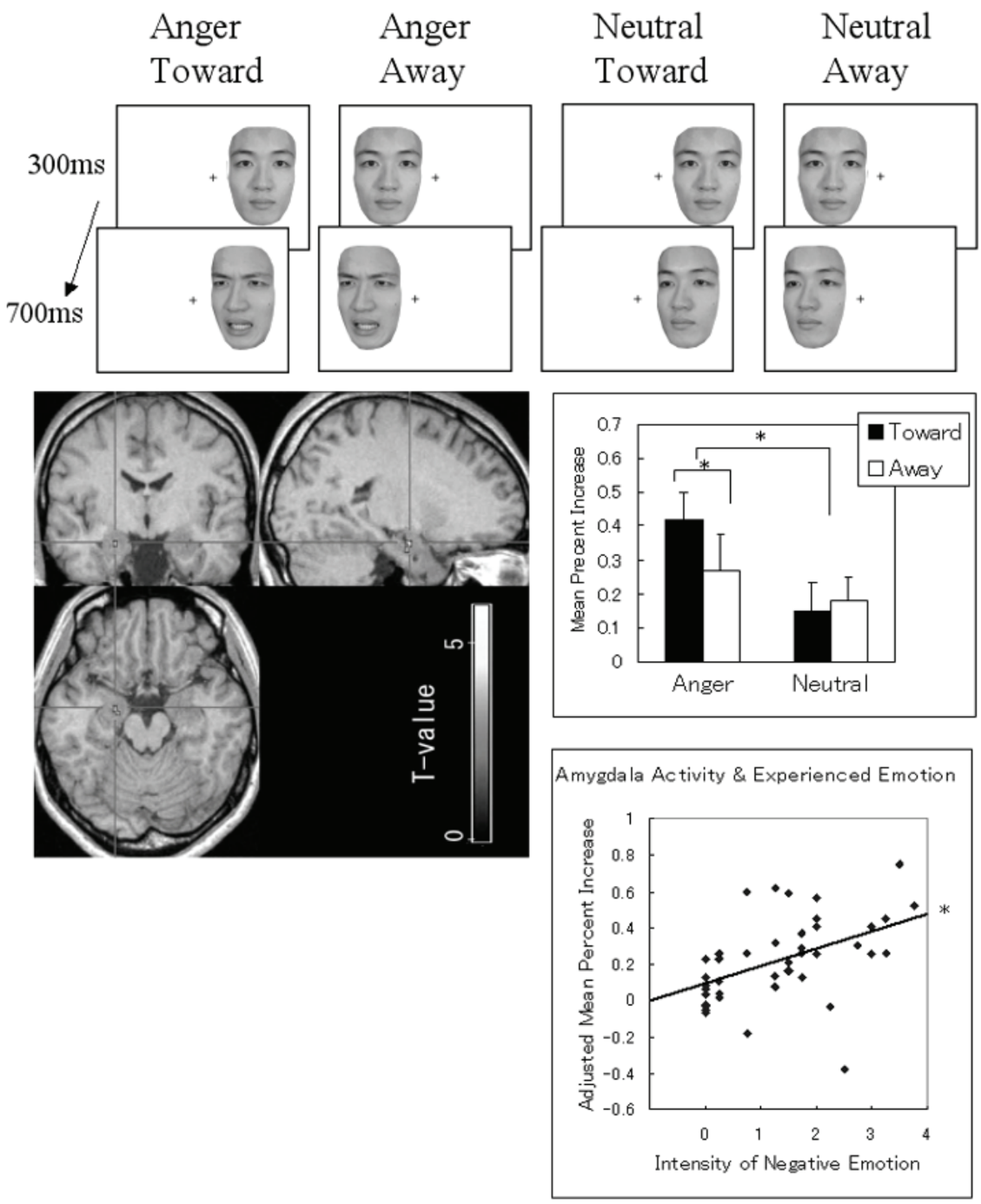


Fig.2. Experiment in the study of Sato et al. (2004).

Top: Examples of stimulus presentations. Four conditions are involved with two expressions (angry and neutral) in two directions (toward and away). Middle left: Areas in the left amygdala demonstrate the interactions of expressions and directions. Middle right: Patterns of activity in the left amygdala. Bottom: Positive relationship between the activity of the left amygdala and the subjective emotional response.

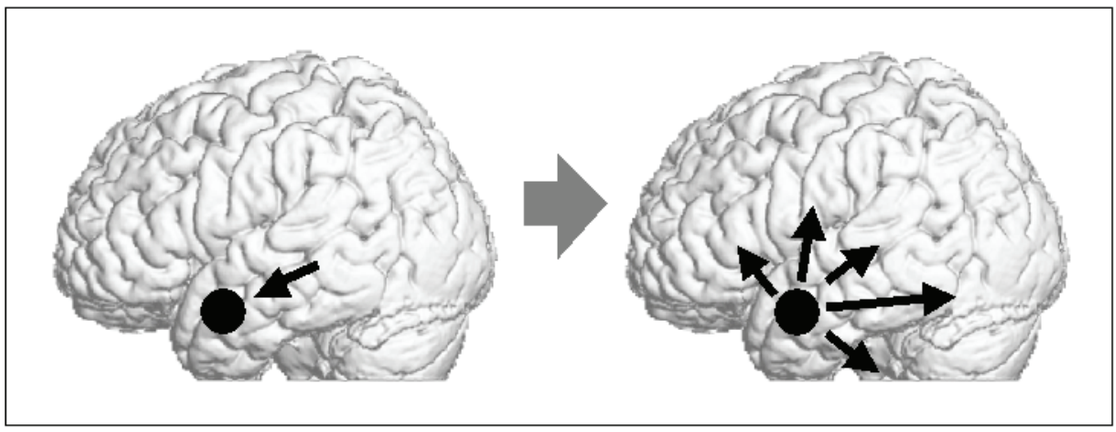


Fig.3. Information processing of the amygdala in emotion

In emotion, the amygdala is involved in the processes that evaluates the adaptive significance of stimuli, and accordingly generates the commands of adaptive responses, which are implemented in other brain regions.

6. Information processing by the amygdala at each emotion-processing stage

In this section, I discuss the details of the processing of emotion in the amygdala during the subprocesses of significance appraisal and response command generation. For the latter, I limit my discussion to three emotional responses as examples: bodily responses, perceptual enhancement, and memory facilitation.

6.1 Subconscious and conscious appraisals of emotion: amygdala activation by sensory inputs via subcortical and cortical routes

Psychological studies have shown that emotion can be elicited with or without the conscious awareness of stimuli (Robinson, 1998).

In addition to evidence of the involvement of the amygdala in processing emotion with conscious awareness (e.g., Sato et al., 2004), some studies have provided evidence that the amygdala is involved in processing emotion without awareness. For example, a neuropsychological study (Kubota et al., 2000) investigated patients with unilateral amygdala damage in which emotionally negative or neutral slides were presented to their unilateral visual fields subliminally. Higher electrodermal responses to negative versus neutral stimuli were observed when stimuli were presented to the intact, but not lesioned, hemispheres. A neuroimaging study (Morris et al., 1999) measured the brain activity when angry facial expressions were presented subliminally with and without fear conditioning. With conditioning, angry faces induced stronger activity of the right amygdala, compared to without conditioning. Regression analyses revealed that the amygdala activity was positively related to the activity of the superior colliculus and pulvinar. Together, these data suggest that the processing of emotions by the amygdala can occur subconsciously and that it may be implemented by sensory input via subcortical routes.

An intracranial field potential recording study in humans (Oya et al. 2002) demonstrated that the amygdala could be activated within as early as 50-150 ms from the stimulus onset in response to emotional stimuli. Since visual awareness has been proposed to be related to the activity of the visual cortices at about 200-300 ms (Treisman & Kanwisher, 1998), the rapid activity of the amygdala could correspond to subconscious emotional processing.
In summary, ample evidence indicates that the amygdala begins to process emotion quickly, before the conscious awareness of stimuli. Since the amygdala has multiple sensory input pathways, including cortical and subcortical projections, it may conduct multistage appraisals of stimulus significance according to the resolution of the sensory inputs.

6.2 Bodily responses of emotion: outputs from the amygdala to the brain stem and hypothalamus

Psychological studies have shown that emotion induces widespread body responses (Levenson, 1991).
The emotional bodily responses are related to the activity of the brain stem and hypothalamus (Buck, 1999). The brain stem consists of functionally different regions, each of which engages with a specific bodily response. For example, the solitary nucleus regulates the activity of the parasympathetic branch of the autonomic nervous system, and the central gray matter is related to freezing behavior. The hypothalamus also consists of different functional regions and is very involved in controlling the body responses by sending output to the brain stem or releasing hormones to the body directly.
Animal research has revealed that the outputs from the amygdala to the brain stem and hypothalamus are related to the emotional body responses. For example, lesion studies in rats demonstrated that the local destruction of the amygdala impaired a specific component of the body responses (LeDoux, 1998). Research in monkeys showed that cooling the amygdala, which produces reversible neuronal lesions, modulated the activity of the hypothalamus neurons for visually presented emotional stimuli (Ono & Nishijo, 1992).
Human neuroimaging studies have also demonstrated the involvement of the amygdala in emotional body responses. For example, an fMRI study (Williams et al., 2001) depicted the brain activity while participants were observing fearful and neutral facial expressions, and measured the electrodermal activity simultaneously. The amygdala was active for fearful expressions inducing clear electrodermal responses, but not for fearful faces failing to elicit electrodermal activity.
In summary, animal and human data indicate that the amygdala outputs to the brain stem and hypothalamus are related to the body responses of emotion.

6.3 Perceptual enhancement by emotion: output from the amygdala to the visual area

Psychological studies have indicated that emotional significance enhances the perception of stimuli (Öhman et al., 2001).
A neuropsychological study (Anderson & Phelps, 2001) confirmed that the amygdala is related to the perceptual enhancement of emotional stimuli. The researchers used the attentional blink phenomenon, in which the identification of the first targets impairs that of the second targets. In normal controls, the transient impairment of conscious awareness for the second targets was attenuated when the second targets were emotional words. In

contrast, in patients with unilateral or bilateral amygdala damage, no difference was observed between emotional and neutral words.

As related evidence, some neuroimaging and electrophysiological studies have reported that emotional stimuli, compared to neutral ones, enhance the activity of the visual cortices, coinciding with the amygdala activity. For example, an fMRI study (Breiter et al., 1996) revealed that that the presentation of fearful and happy faces activated the ventral visual cortices and amygdala more strongly than neutral faces. Sato et al. (2001) recorded event-related potential (ERP) while viewing fearful, happy, and neutral facial expressions. The fearful and happy expressions induced higher activity over the posterior temporal areas during 200–300 ms after stimulus onset compared to neutral expressions. Independent component analyses indicated that the negative potential of the posterior cortices was coupled with positive potential of the anterior midline region functionally, implying limbic system activity. One can interpret these data as showing that the rapid enhancement of the visual area activity for emotional stimuli is realized by the direct output from the amygdala. The activity of the visual area within 200–300 ms has been suggested as being related to perceptual awareness (Treisman & Kanwisher, 1998); hence, this heightened activity of the visual area might cause the perceptual enhancement of emotional stimuli.

In summary, human data suggest that the amygdala is related to perceptual enhancement by emotion, possibly via the rapid output from the amygdala to the visual area.

6.4 Memory facilitation by emotion: outputs from the amygdala to the hippocampus, basal ganglion and neocortex

Psychological studies have suggested that emotional significance enhances the memory performance for stimuli (Bradley et al., 1992).

Research with rats has indicated that the influence of the amygdala on other brain regions is related to this memory facilitation. A series of studies by McGaugh and his colleagues (1999) revealed that the learning of avoidance behaviors to emotionally aversive stimuli was facilitated by the electric stimulation of the amygdala; in contrast, when the amygdala was damaged, the performance became poorer. The stimulation of the amygdala affected both spatial memory and procedural memory. Since these two memory functions are related to the hippocampus and basal ganglion, respectively, the data suggest that the amygdala influences these regions. Electrophysiological recordings further revealed that amygdala activity modulated the activity of the neocortex related to memory consolidation.

Human data have also indicated the involvement of the amygdala in memory enhancement by emotion. For example, a neuropsychological study (Adolphs et al., 1997) investigated the memory performance for a story including an emotional scene. While the normal controls performed better for the emotional scene than for other scenes, the patients with bilateral amygdala damage did not show an advantage regarding the emotional scene. A neuroimaging study (Cahill et al., 1996) measured the brain activity while presenting unpleasant and neutral films and subsequently tested memory performance. The memory performance was better for the unpleasant films than for the neutral ones, and the amygdala activity was positively related to the memory performance for the unpleasant films.

Together, the evidence indicates that the amygdala sends outputs to other brain regions, including the hippocampus, basal ganglion, and neocortex, facilitating the memory performance for emotional stimuli.

7. Conclusion

This article reviewed research on the amygdala and discussed its role in emotion. Psychological studies have revealed that emotion is a series of information processes that evaluates the adaptive significance of stimuli and generates adaptive responses accordingly. Neuroscientific evidence indicates that in terms of emotion, the amygdala is involved in appraising the significance of stimuli and generating response commands for other regions. Emotion is appraised rapidly in the amygdala through sensory inputs via subcortical routes, before the conscious awareness of stimuli. The outputs from the amygdala induce diverse emotional responses by activating other brain regions.

Although this article focused on the amygdala, other brain regions appear to process emotion similarly, including the orbitofrontal cortex and nucleus accumbens. Evidence suggests that these regions are related to different sorts of appraisals of emotion and different emotional responses. As the amygdala and these regions have close interconnections, these areas may form a neural network and thus be involved in more complex emotion processing.

Many issues remain to be clarified regarding the role of the amygdala in emotion. For example, no consensus exists as to what types of emotion involve the amygdala. However, neuroscientific studies on emotion are making dramatic progress. As our understanding of the brain mechanisms, especially of the amygdala, advances, we will gain more profound knowledge regarding the mechanisms of emotion.

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Affective Computing

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This book provides an overview of state of the art research in Affective Computing. It presents new ideas, original results and practical experiences in this increasingly important research field. The book consists of 23 chapters categorized into four sections. Since one of the most important means of human communication is facial expression, the first section of this book (Chapters 1 to 7) presents a research on synthesis and recognition of facial expressions. Given that we not only use the face but also body movements to express ourselves, in the second section (Chapters 8 to 11) we present a research on perception and generation of emotional expressions by using full-body motions. The third section of the book (Chapters 12 to 16) presents computational models on emotion, as well as findings from neuroscience research. In the last section of the book (Chapters 17 to 22) we present applications related to affective computing.

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