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Motivational Salience: Amygdala Tuning From Traits, Needs, Values, and Goals

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Abstract

Based on a basic emotions perspective, a dominant view in psychology is that the primary function of the amygdala is to govern the emotion of fear. In this view, the amygdala is necessary for a person to feel afraid, and when amygdala activity is detected, one can infer that a person is feeling afraid or threatened. In this paper, we review current research on amygdala function that calls into question this threat-specific view and propose a more general view of amygdala functioning based on appraisal theory and psychological constructivism. Specifically, we examine the hypothesis that the amygdala is involved in processing stimulus relevance for the goals and motivations of the perceiver. Thus, although threatening stimuli are almost always considered a relevant stimulus, novel, ambiguous, and extremely positive stimuli can also be relevant for different people in different situations. Once deemed relevant, the amygdala guides processing to orchestrate an appropriate response.

Keywords

amygdala, appraisal, emotion, fear, goals, motivation, perception

> "We can tell how someone is feeling, and we can specifically identify responses associated with sociopathic tendencies. Here we determined that the defendant was racist [with] extreme accuracy. In this case, we showed Mr. Bass pictures of people from various races, and then we measured the response in the part of his brain that controls fear. It's called the amygdala . . . Officer Bass perceives Black men as threatening."
>
> *Boston Legal*, Season 4, Episode 7, "Attack of the Xenophobes" (Kelley, Turk, & Terlesky, 2007)

> In anticipation of the 2008 presidential election, we used functional magnetic resonance imaging to watch the brains of a group of swing voters as they responded to the leading presidential candidates . . . When we showed subjects the words "Democrat," "Republican" and "independent," they exhibited high levels of activity in the part of the brain called the amygdala, indicating anxiety.
>
> *New York Times*, "This is Your Brain on Politics," November 11, 2007 (Iacoboni et al., 2007)

The quotes above articulate a dominant perspective concerning how emotion is represented in the brain. In this view, the brain is organized into modules that provide basic psychological processes, and particular brain structures give rise to different emotional states. This perspective is guided conceptually by basic emotion theories, which assume that there are a number of distinct, universal emotions—such as anger, fear, sadness, happiness, disgust, or surprise (Ekman, 1992)—that elicit response patterns driven by specific neural response systems. From this perspective, the function of the amygdala is to govern fear, and thus, whenever we observe an amygdala response, we can make the reverse inference that a person is feeling fear or at the very least is processing a stimulus as being potentially threatening. Following this reasoning, studies over the past decade have shown an association between amygdala activation and the perception of social out-group members, leading to conclusions that provide the basis of how the neuroscience of prejudice can inform legal opinion.

In this article, we review research on amygdala function that calls into question this threat-specific view and propose a more general view based on appraisal theory and psychological constructivism. Specifically, we review literature that suggests that the amygdala is involved in processing the relevance of a stimulus for the goals and motivations of the perceiver. Once a stimulus is deemed relevant through either bottom-up or top-down processes, the amygdala is well situated anatomically to enhance the salience of the stimulus and prepare an

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adaptive whole-body response to a change in the environment.[1] In this view, threatening stimuli are only one type of relevant stimuli. Novel, ambiguous, and positive stimuli can also be relevant for different people in different situations.

Classic Amygdala Findings, Interpretations, and Challenges

An examination of the anatomic connections with the amygdala suggests that this region is well suited for automatic vigilance and organized response functions (Davis & Whalen, 2001). Specifically, the amygdala has widespread connections to areas associated with sensory processing at all stages of the perceptual pathways as well as regions involved in autonomic/visceral activation (see Freese & Amaral, 2009). This connectivity enables the amygdala to receive rich sensory information and strengthens the neural representation of emotional stimuli via feedback signals from the amygdala on sensory pathways (see Fig. 1). Thus, following amygdala activation, greater attention can be directed to the stimulus while the body prepares for immediate action. Brain imaging studies have revealed increased neural responses to many different classes of emotional stimuli, both in early sensory areas such as the primary visual cortex and in higher-level regions such as the fusiform face area. Consistent with the idea that the amygdala plays a causal role, the enhanced neural responses toward emotional information are not observed in patients with amygdala damage. As a result of this enhanced neural representation, emotional stimuli have preferential access to awareness. For example, in the attentional blink task, the detection of a target word in a rapid serial visual stream is usually impaired when the target occurs shortly after another target. However, this deficit is greatly attenuated for emotional targets. In healthy subjects, the behavioral facilitation for emotional information is related to trial-by-trial fluctuations in the amygdala and visual cortex. In contrast, no facilitated access to awareness for emotional stimuli is observed in patients with amygdala lesions (see Vuilleumier & Brosch, 2009).

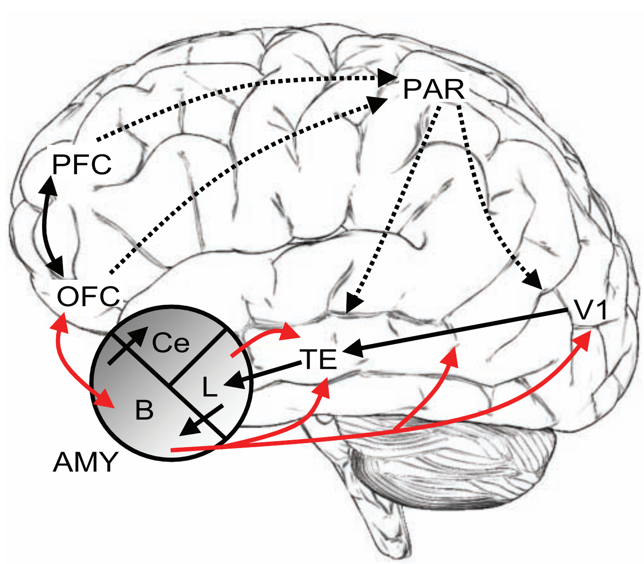

Fig. 1. Brain areas involved in motivational salience. The amygdala (AMY) has dense reciprocal connections with widespread regions in the cortex, including all stages of the perceptual pathways (primary visual cortex, V1, inferior temporal cortex, TE) as well as prefrontal regions (orbitofrontal cortex, OFC, prefrontal cortex, PFC). This connectivity enables the amygdala to receive rich sensory information and to strengthen the neural representation of emotional stimuli via feedback to and from sensory pathways. Most of these projections arise from the basal nucleus of the amygdala (B). By contrast, most visual inputs to the amygdala project to the lateral nucleus (L), which then projects to the basal nucleus and back to higher-level areas only. In addition to its connectivity to sensory regions, the amygdala has multiple connections to prefrontal areas, which relay amygdala input to regions involved in more deliberate forms of decision making and allow for modulations of amygdala activity based on more complex motivational contingencies. Thus, following amygdala activation, multiple brain systems can dynamically reorganize to appropriately deal with the current environment. PAR = parietal cortex. Figure reprinted from "Interactions of emotion and attention in perception," by P. Vuilleumier, & T. Brosch, 2009, in M. S. Gazzaniga (Ed.), *The cognitive neurosciences IV*, p. 928, Cambridge. MA: MIT Press. Copyright 2009, MIT Press. Reprinted with permission.

In addition to its connectivity to sensory regions, the amygdala has multiple connections to prefrontal areas, receiving from and relaying information to areas of orbitofrontal, insular, and lateral prefrontal cortices (Stefanacci & Amaral, 2000). These reciprocal connections allow information processed in the amygdala to be used by regions involved in more deliberate forms of decision making and allow amygdala activation to be modulated to take into consideration the entire state of the organism. Thus, following amygdala activation, multiple brain systems can dynamically reorganize to appropriately deal with the current environment.

Although the amygdala's role in vigilance is well established, the specificity of this response is less well understood. Traditionally, the amygdala has been considered to play a critical role in the detection and processing of threatening cues and the generation of a fear response (Phelps & LeDoux, 2005)—a conceptualization that dates to 1937, when it was first demonstrated that lesions to the temporal lobes led to reduced avoidance of potentially threatening stimuli (Kluver & Bucy, 1937). Further work in patients with bilateral amygdala lesions confirmed the critical role of the amygdala in the processing of fear, demonstrating that these patients have impairments in processes such as the acquisition of conditioned fear responses, the recognition of fearful facial expressions, and the conscious experience of fear (see Feinstein, Adolphs, Damasio, & Tranel, 2011). Replicating these results in non-brain-damaged populations, research using functional magnetic resonance imaging (fMRI) has shown that the amygdala is involved in the detection of threat in many stimulus modalities, including the perception of fear expressions in faces or voices, cognitive representations of fear, threat-related words, and aversive odors. Given this body of research, it is not surprising that a one-to-one correspondence between amygdala activation and threat detection has been assumed. Indeed, the function of the amygdala has been described as a "fear module" exclusively dedicated to the automatic detection of fear-relevant information and the orchestration of adaptive responses (see Öhman, 2005).

Yet, this suggestion that the amygdala's role in evaluation is valence specific has been called into question. Specifically, several studies have since shown that the amygdala is sensitive not only to fearful or negative information but also to positive information (Hamann, Ely, Hoffman, & Kilts, 2002). Furthermore, in addition to its role in fear learning, the amygdala has been implicated in the learning of stimulus–reward associations (Baxter & Murray, 2002). Hamann and colleagues (2002) replicated the finding that the amygdala responds not only to positive and negative stimuli but also to unusual or interesting stimuli, suggesting that it serves a more general function than just processing valence. Further, studies that have independently manipulated valence and intensity (Anderson et al., 2003) or statistically examined the contributions of the two (Cunningham, Raye, & Johnson, 2004) have suggested that activity may be more related to intensity than to valence. Consistent with this idea, patients with bilateral amygdala damage have impaired recognition of emotional arousal while recognition of valence remains intact (Adolphs, Russell, & Tranel, 1999). With this interpretation, novel or ambiguous stimuli result in greater amygdala activation presumably because uncertain events are more arousing (or potentially more threatening) than certain events are.

Relevance Detection and Modulation of Salience

The assumption underlying the analytical approach of these studies is that there is a consistent pattern of amygdala activation across participants. Yet, a careful analysis of the subject-by-subject patterns of amygdala response reveals something very different—specifically, very few individual patterns look like the average. Whereas some participants do show a pattern of greater amygdala response to negative and positive stimuli than to neutral stimuli, others show heightened responses only to negative stimuli, and still others show the opposite response, with greatest activation to positive stimuli. These data may suggest that amygdala activation may not "mean" the same thing for each participant and that the psychological state of the person may be key to understanding the particular pattern of results in any given moment.

One way to explain both the general patterns of amygdala response and also the variation in the response is by conceptualizing the amygdala as involved in the processing of motivationally relevant stimuli (e.g., Sander, Grafman, & Zalla, 2003). Following this initial relevance evaluation, additional resources are recruited to facilitate situationally appropriate responses (Brosch, Sander, Pourtois, & Scherer, 2008). This suggestion is based on appraisal theories of emotion (see Ellsworth & Scherer, 2003), which, in stark contrast to the rather inflexible pattern-matching mechanism put forward by basic theories of emotion, emphasize the importance of the subjective evaluation of a stimulus according to its importance for the individual. Thus, the amygdala functions, at least in part, as part of a larger affect system automatically informing us about what is important in the environment and then facilitating the modulation of appropriate perceptual, attentional, autonomic, or cognitive/conceptual processes to respond to the challenges or opportunities that are present. In this view, differences in amygdala responding to various situations and differences between people are not noise in the data but rather the critical variations to be understood. Specifically, we expect that amygdala activation should vary as a function of the needs, goals, and values of the organism.

Thus, motivational relevance of stimuli can be defined as usefulness for any momentary motivational state of the individual. Because multiple goals can be important, the salience and priority of specific needs, goals, and values are important for shaping a response. Motivational contingencies, and thus the relevance of a given stimulus, may change continuously. For example, when one is thirsty, water (an appetitive stimulus) will be more relevant, whereas when one is in a dangerous neighborhood, potential criminals (an aversive stimulus) will be more relevant. Consistent with this idea, a recent study investigated neural mechanisms underlying attention toward food in participants both when hungry and satiated, thus varying the motivational relevance of the food stimuli within participants (Mohanty, Gitelman, Small, & Mesulam, 2008). When hungry, participants showed not only increased amygdala activation to pictures of food but also faster attentional orienting toward food cues and increased connectivity between limbic areas and parietal attention regions subserving attentional shifts, compared to when they were satiated.

At a general level of analysis, it is likely that through direct experience or genetic predispositions, people come to have different chronic expectations about the world (benevolent or malevolent) and how to best interact with it. These biases provide cues to what is important for an individual and can provide a tuning for the affective system. What one thinks should be attended to in a dangerous world is quite different from what should be attended to in a world of opportunities.[2] Providing evidence for this, individual differences in neuroticism—a trait characterized by emotional lability and attention to negative outcomes—have been shown to be associated with greater amygdala activation to negative compared to positive stimuli (Harenski, Kim, & Hamann, 2009). Likewise, people higher in extraversion, a personality characteristic associated with enthusiasm and sociability, have a greater amygdala response to pleasant photographs or happy faces (Canli, Sivers, Whitfield, Gotlib, & Gabrieli, 2002). Moreover, individual differences in promotion focus (a motivational system attuned to rewards) predicted greater amygdala activation to positive stimuli, whereas individual differences in prevention focus (a motivational system attuned to punishments) predicted greater activation to negative stimuli (Cunningham, Raye, & Johnson, 2005). Values are stable motivational aspects of the self-schemata that determine what individuals regard as desirable and important and which concrete goals they choose to pursue (Brosch, Coppin, Schwartz, & Sander, in press). In a resource-distribution task, participants who endorsed values related to the pursuit of self-interested action showed increased amygdala activation toward opportunities to increase their personal financial gain and were also less likely to donate money to a charitable organization than participants who endorsed more altruistic values (Brosch, Coppin, Scherer, Schwartz, & Sander, 2011).

Yet, although this tuning occurs, the strategies that people use to deal with emotional reactivity can differ vastly. For example, if someone believes the world to be threatening, he or she can deal with this construal by becoming increasingly vigilant to certain stimulus features to ensure that all potential threats are detected. Alternatively, he or she can become avoidant and choose to not engage with the world (decreasing the possibility that a negative event has the opportunity to occur). Thus, the means by which a person seeks to accomplish a goal may also modulate amygdala responses, as different situations may more or less afford a preferred response. To test this, Cunningham, Arbuckle, Jahn, Mowrer, and Abduljalil (2010) examined two neuroticism aspects (volatility/withdrawal) and their relationship to amygdala activation. Previous research has suggested that Neuroticism-Volatility is a function of the fight–flight–freeze system and that attention toward cues signals negativity, whereas Neuroticism-Withdrawal has been linked to the behavioral inhibition system and passive avoidance (DeYoung, Quilty, & Peterson, 2007). Participants with higher Neuroticism-Volatility scores had increased amygdala activation to both approached and avoided negative stimuli, whereas participants with higher Neuroticism-Withdrawal scores were insensitive to valence but showed increased amygdala activation when asked to approach stimuli. These data provide further support for the motivational salience hypothesis by demonstrating that both the ends and means of goal pursuit are important for determining relevance and thereby shaping the amygdala response.

If changes in chronic strategies are important for determining the affective meaning of a stimulus, more abstract goals and values should also be able to shape neural responses. To examine the flexibility of this response for more abstract goals, Cunningham, Van Bavel, and Johnsen (2008) presented participants with famous names and asked them to focus on either the positive or negative aspects of the person. Activity in the amygdala bilaterally was found to vary as a function of evaluative fit. That is, when focusing on negativity, greater amygdala activity was associated with participants' negativity ratings but not with their positivity ratings. The opposite pattern was found for the positive-focus condition, such that greater activity was observed in these same regions to ratings of positivity than to ratings of negativity. Critically, these effects were observed within subjects, suggesting that top-down influences on motivational relevance can alter responses within seconds, resulting in qualitatively different patterns of amygdala responses. Similarly, Ousdal and colleagues (2008) observed increased amygdala activation toward simple letter stimuli—which are usually considered nonemotional and are not expected to activate the amygdala—when the letters were targets in a go/no-go task and thus behaviorally relevant to participants' performance.

Returning to the opening of this article, one area in which amygdala activation has been used to infer affective states has been the study of prejudice. Studies using fMRI to study racial attitudes have suggested a role for the amygdala in the processing of threat associated with automatic prejudice (Cunningham et al., 2004; Lieberman, Hariri, Jarcho, Eisenberger, & Bookheimer, 2005; Phelps et al., 2000). Yet, if the amygdala responds to motivational relevant stimuli rather than to threat per se, it may be possible to reverse these effects and find greater amygdala activity to in-group members to the extent that such people are deemed motivationally relevant. Situations like this should not be unexpected—people who accurately identify, value, and cooperate with in-group members enjoy numerous functional benefits, including the fulfillment of their basic psychological needs (Allport, 1954). To test for this, Van Bavel, Packer, and Cunningham (2008) randomly assigned participants to a mixed-race team and used fMRI to identify brain regions involved in processing novel in-group and out-group members. Whereas previous research on intergroup perception found amygdala activity—typically interpreted as negativity—in response to social out-groups, we found greater activity in the amygdala when participants viewed novel *in-group* faces than when they viewed novel *out-group* faces.

Conclusions

Together, this research suggests that the affect system in general, and the amygdala in particular, is more dynamic than once thought. Although the amygdala is involved in rapid processing of stimuli, it is not necessarily the case that this activation is specific to fear, nor does it allow the inference that someone is experiencing fear. Rather, this processing may reflect an early stimulus evaluation check that determines the relevance of a stimulus with respect to one's ongoing motivational state. Thus, for different people in different situations, amygdala activation may be part of their affective responses, but the outcomes of those responses may be vastly different. These findings question the usefulness of strong forms of basic emotion theory for understanding affective processes and suggest that greater attention to understanding how emotions are constructed from more elemental cognitive processes may be required (Barrett, 2006; Ellsworth & Scherer, 2003).

Recommended Reading

Cunningham, W. A., Van Bavel, J. J., & Johnsen, I. R. (2008). (See References). A study demonstrating that the relationship between valence and amygdala processing is modulated by evaluative processing goals.

Phelps, E. A., & LeDoux, J. E. (2005). (See References). A review of the human and animal work on amygdala function.

Sander, D., Grafman, J., & Zalla, T. (2003). (See References). A review paper making the argument that the amygdala is involved in relevance detection.

Van Bavel, J. J., Packer, D. J., & Cunningham, W. A. (2008). (See References). Shows that the amygdala can respond to in-group members when motivationally relevant.

Vuilleumier, P., & Brosch, T. (2009). (See References). Provides a review of the literature demonstrating how emotion (and the amygdala) shape perceptual processes.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Notes

1. Although we highlight top-down factors, we do not suggest that amygdala activation is exclusively shaped by current motivational concerns. Stimulus-driven bottom-up processing certainly also plays an important role, as demonstrated, for example, by the finding that the amygdala response to the untrustworthiness of faces is better predicted by consensus trustworthiness ratings of a large group of participants (arguably reflecting bottom-up structural properties of the faces) than by the individual trustworthiness ratings given by the person in the scanner (Engell, Haxby, & Todorov, 2007). We argue that both bottom-up and top-down factors need to be taken into account for an understanding of the functional profile of the amygdala.

2. This is not to suggest that one's theories are a veridical representation of the dangers and opportunities present in the environment, but rather to suggest that once one has this representation, the affect system operates as if it is appropriate.

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