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#### Review

# The role of the amygdala in emotional processing: A quantitative meta-analysis of functional neuroimaging studies

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#### Abstract

Functional neuroimaging studies have provided strong support for a critical role of the amygdala in emotional processing. However, several controversies remain in terms of whether different factors—such as sex, valence and stimulus type—have an effect on the magnitude and lateralization of amygdala responses. To address these issues, we conducted a meta-analysis of functional neuroimaging studies of visual emotional perception that reported amygdala activation. Critically, unlike previous neuroimaging meta-analyses, we took into account the magnitude (effect size) and reliability (variance) associated with each of the activations. Our results confirm that the amygdala responds to both positive and negative stimuli, with a preference for faces depicting emotional expressions. We did not find evidence for amygdala lateralization as a function of sex or valence. Instead, our findings provide strong support for a functional dissociation between left and right amygdala in terms of temporal dynamics. Taken together, results from this meta-analysis shed new light on several of the models proposed in the literature regarding the neural basis of emotional processing.

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#### 1. Introduction

The field of human affective neuroscience has greatly benefited from the use of functional neuroimaging techniques. In particular, results from several hundred studies in healthy participants have helped delineate the neural circuitry involved in emotional processing, as well as the interactions between emotion and other cognitive processes, such as attention, memory and decision-making. Overall, these studies have confirmed the critical role of the amygdala in emotion, in agreement with findings from research on experimental animals (LeDoux, 2000) and neurological patients (Adolphs and Spezio, 2006). Furthermore, these studies have allowed researchers to test and refine existing models of amygdala function, and to develop new ones.

For instance, a widely held view is that the amygdala is a key component of a neural system specialized for the rapid and automatic evaluation of stimuli that signal potential threat or danger in the immediate environment (Adolphs et al., 1999). However, other researchers have proposed a more general role of this structure in the processing of signals of distress (Blair et al., 1999), including other negative emotions such as sadness, or in the processing of signals that indicate potentially important environmental information that must be disambiguated (Whalen et al., 2001) (e.g., facial expressions of surprise (Kim et al., 2003)). Finally, a recent model postulates that the human amygdala acts as a "relevance detector," involved in the processing of biologically relevant stimuli, regardless of their valence (Sander et al., 2003).

In addition, several theories have been proposed regarding possible hemispheric differences in emotion, thus raising the possibility of a differential involvement of the left and right amygdala in emotional processing. One of the oldest models of emotion lateralization, first proposed by Luys in 1881, posits that the right hemisphere is more involved than the left in emotional processing in general, including both positive and negative emotions (Sackeim and Gur, 1978; Schwartz et al., 1975). Another one suggests a hemispheric dissociation based on emotional valence, namely preferential processing of positive and negative information by the left and right hemispheres, respectively (e.g., Sackeim et al., 1982). This lateralization theory, especially in relation to the role of prefrontal cortex, has been refined by Davidson and colleagues, who proposed a hemispheric differentiation in terms of approach and

withdrawal behavior, rather than valence (Davidson, 1984; Davidson et al., 1990; Sackeim et al., 1982).

More specific to the amygdala, a lateralization model has been proposed based on the established hemispheric differences associated with language. Namely, left amygdala would be involved in the processing of semantic material (e.g., scripts, sentences or words), whereas non-semantic information (e.g., faces, pictures) would engage the right amygdala (Markowitsch, 1998; Phelps et al., 2001).

Finally, more recent models have been proposed in terms of the temporal dynamics of the amygdala in response to emotional stimuli, based on its differential patterns of habituation (Phillips et al., 2001; Whalen et al., 1998; Wright et al., 2001). For instance, Wright et al. (2003) have proposed that whereas the right amygdala is involved in the rapid detection of emotional stimuli, the left amygdala plays a role in the more elaborate stimulus evaluation (see also Markowitsch, 1998). In a similar vein, Glascher and Adolphs (2003) suggested that the right amygdala is engaged in the initial, possibly automatic detection of an emotional stimulus, followed by a more detailed and specific analysis of variations in the magnitude of arousal associated with the stimulus mediated by the left amygdala.

In addition, sex differences in amygdala responses to emotional stimuli have also been proposed, specifically, a stronger and more bilateral amygdala activity in women than in men (Hamann, 2005; Killgore and Yurgelun-Todd, 2001). These putative neural differences are thought to underlie the often reported enhanced emotional reactivity in women (Hall and Matsumoto, 2004).

Although all these theories have received considerable support from the neuroimaging literature, many other studies have yielded contradictory results. The reasons for these discrepancies remain to be determined, especially given the large differences in methodology, paradigms, population, stimuli, and other experimental parameters across studies. One way to avoid these potential confounds and draw conclusions from disparate studies is through the use of meta-analytical approaches. This "analysis of analyses" (Glass, 1976) combines the findings of many studies investigating a common topic within a unifying framework. This technique is particularly well-suited for functional neuroimaging studies, where different paradigms are used and the number of statistical results typically reported (i.e., voxels activated in a particular contrast) can be quite large, making it difficult to interpret without the aid of a quantitative instrument.

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