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Review article

Perceiving emotional expressions in others: Activation likelihood estimation meta-analyses of explicit evaluation, passive perception and incidental perception of emotions

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ABSTRACT

We conducted a series of activation likelihood estimation (ALE) meta-analyses to determine the commonalities and distinctions between separate levels of emotion perception, namely incidental perception, passive perception, and explicit evaluation of emotional expressions. Pooling together more than 180 neuroimaging experiments using facial, vocal or body expressions, our results are threefold. First, explicitly evaluating the emotions of others recruits brain regions associated with the sensory processing of expressions, such as the inferior occipital gyrus, middle fusiform gyrus and the superior temporal gyrus, and brain regions involved in low-level and high-level mindreading, namely the posterior superior temporal sulcus, the inferior frontal cortex and dorsomedial frontal cortex. Second, we show that only the sensory regions were also consistently active during the passive perception of emotional expressions. Third, we show that the brain regions involved in mindreading were active during the explicit evaluation of both facial and vocal expressions. We discuss these results in light of the existing literature and conclude by proposing a cognitive model for perceiving and evaluating the emotions of others.

Contents

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1. Introduction

We can think of emotion perception as a spectrum that runs from subliminal perception (i.e. without conscious awareness) and incidental processing (i.e. perceiving the emotion despite focusing on another attribute of the individual, such as gender) to passive perception and the explicit identification of a person's emotion. It is at this end of the spectrum that emotion perception requires a conscious deliberative decision about the likelihood of a particular emotional state (Adolphs, 2002). This is especially true in the case of noisy or ambiguous cues (Bajaj et al., 2013; Donhauser et al., 2013; Frühholz et al., 2009b; Scocchia et al., 2014). Furthermore, explicit emotion identification can be achieved by way of two mechanisms which differ on several accounts, such as the type of input that they use (Sabbagh et al., 2004; Tager-Flusberg and Sullivan, 2000), cognitive processes (Samson, 2009), and brain networks recruited (Spunt and Lieberman, 2012). Specifically, *emotion evaluation* is accomplished based on immediately observable perceptual cues (e.g. tone of voice, facial expressions), whereas *emotion attribution* relies on situational information in the absence of observable expressions. As such, emotion evaluation depends on domain-general cognitive processes (Beer and Ochsner, 2006), including discrimination (i.e. a smile from a frown) and categorization, and relies on brain regions such as the posterior superior temporal sulcus (Allison et al., 2000). Emotion attribution, on the other hand, depends on extended conceptual knowledge (Ong et al., 2015) in the form of person knowledge (e.g. someone's idiosyncrasies) and social knowledge (i.e. a lay theory on the relations between situations, emotions and behaviors; e.g. "not having what you want causes sadness"), and is subserved by brain regions such as the medial frontal cortex and inferior frontal cortex (Herbet et al., 2013).

While *emotion attribution*, as described above, has been associated with mindreading or theory of mind abilities (Addington et al., 2006; Bora et al., 2006; Sabbagh et al., 2004), much debate revolves around the computational nature of *emotion evaluation*. For example, some researchers favor a simulation-based approach (i.e. people use their own minds and body to simulate and understand others' emotions; see (Goldman, 2008)), while others argue for the use of a lay theory (i.e. people use abstract causal principles about the world to understand and explain others' emotions; see (Skerry and Saxe, 2014; Tager-Flusberg and Sullivan, 2000)). Yet other authors suggest that emotion perception may equally induce affective reactions in the observer and trigger inferential processes about the perceived person's state of mind and intentions (Van Kleef, 2009; Van Kleef et al., 2010), especially when the perceived emotion is directed towards the observer (Van Kleef, 2010). In the broadest sense, emotions are cases of mental states which can be reliably decoded from observable features such as facial expressions and vocal expressions (Sabbagh et al., 2004; Tager-Flusberg and Sullivan, 2000). At the very least, emotions serve as proxy for beliefs and desires (Reisenzein, 2009; Wellman and Woolley, 1990). For instance, a happy expression reveals that a person's desire has been fulfilled, whereas a surprised expression reveals that the person held a false belief.

To date, there have been no systematic reviews of the evaluations that people make about the emotions they perceive in others, either at a behavioral or at a neural level. While several meta-analyses on emotion processing already exist from aggregated neuroimaging data, we argue that they suffer from conceptual and methodological shortcomings. Specifically, meta-analyses on emotions have grouped together distinct levels of emotion perception (i.e. incidental perception, passive perception, and explicit evaluation; see (Fusar-Poli et al., 2009; Phan et al., 2002; Wager et al., 2003)), emotion perception with emotion experience (Kober et al., 2008; Vytal and Hamann, 2010), and emotion perception with memory for emotional stimuli (Murphy et al., 2003). However, empirical studies across different perceptual modalities (Cunningham et al., 2004; Frühholz et al., 2011; Habel et al., 2007; Lane, 2008; Taylor et al., 2003) strongly suggest that passive perception, incidental perception, and explicit emotion evaluation represent different forms of emotion perception with distinct brain mechanisms. Consequently, aggregating different levels of emotion processing will likely lead to misinterpretations.

In this study, we conducted a series of meta-analyses that address these shortcomings by separately compiling neuroimaging studies on (explicit) emotion evaluation, passive perception, and incidental perception of emotions. The main goal was to reveal the brain structures associated with evaluating and deliberating over the emotional expressions of others. In line with the literature, we hypothesized that emotion evaluation stands at the interface between perceptual processing and mental states inference. Accordingly, we expected to reveal brain regions associated with processing the perceptual cues from observable stimuli depending on stimulus modality (e.g. fusiform gyri for perceiving faces; superior temporal gyrus for perceiving voices), as well as brain regions associated with mentalizing about others (e.g. medial frontal cortex, inferior frontal cortex).