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Research report

Neural signatures of conscious and unconscious emotional face processing in human infants

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ABSTRACT

Human adults can process emotional information both with and without conscious awareness, and it has been suggested that the two processes rely on partly distinct brain mechanisms. However, the developmental origins of these brain processes are unknown. In the present event-related brain potential (ERP) study, we examined the brain responses of 7-month-old infants in response to subliminally (50 and 100 msec) and supraliminally (500 msec) presented happy and fearful facial expressions. Our results revealed that infants' brain responses (Pb and Nc) over central electrodes distinguished between emotions irrespective of stimulus duration, whereas the discrimination between emotions at occipital electrodes (N290 and P400) only occurred when faces were presented supraliminally (above threshold). This suggests that early in development the human brain not only discriminates between happy and fearful facial expressions irrespective of conscious perception, but also that, similar to adults, supraliminal and subliminal emotion processing relies on distinct neural processes. Our data further suggest that the processing of emotional facial expressions differs across infants depending on their behaviorally shown perceptual sensitivity. The current ERP findings suggest that distinct brain processes underpinning conscious and unconscious emotion perception emerge early in ontogeny and can therefore be seen as a key feature of human social functioning.

1. Introduction

The ability to perceive and distinguish between emotional facial expressions of others is of critical importance for adaptive social behavior as it helps us predict others' actions and guide our own behavior during social interactions (Adolphs, 2002; Frith, 2009). Given the significance of this ability it is not surprising that it not only relies on the conscious perception of others' emotional states, by which inferences about inner state and future behavior of another person can be drawn, but that the detection of emotional expressions in others occurs independent of conscious awareness (Morris, Ohman, & Dolan, 1999; Tamietto & de Gelder, 2010).

From a neuroscience perspective, prior work examining event-related brain potentials (ERPs) in human adults suggests that the responding to emotional information relies on

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distinct brain processes that (a) depend on conscious perception (supraliminal processing) and (b) are independent of conscious perception (both supra- and subliminal processing). Specifically, the processing of perceptually unconscious emotional information is characterized by an enhanced N2 for negative facial expressions (Kiss & Eimer, 2008; Liddell, Williams, Rathjen, Shevrin, & Gordon, 2004; Williams et al., 2004). The adult human brain thus responds to evolutionarily significant stimuli such as negative facial expressions, even in the absence of conscious awareness (Cacioppo & Berntson, 1999; Liddell et al., 2004). On the contrary, conscious processing of emotional faces involves a more detailed structural analysis of faces, as indexed by emotion effects on the N170, which only occur when the correct emotion is successfully recognized (Japee, Crocker, Carver, Pessoa, & Ungerleider, 2009; Smith, 2012). Moreover, consciously perceived emotional expressions elicit enhanced P3 amplitudes in response to fearful facial expressions (Kiss & Eimer, 2008; Liddell et al., 2004). This suggests that the conscious perception of fearful expressions results in a controlled evaluation of the stimulus content, which is associated with deeper memory encoding (Polich, 2007). In addition, the processing of emotional faces independent of conscious perception also involves shared neural mechanisms. In response to both sub- and supraliminal facial expressions, an enhanced anterior positivity for negative compared to neutral facial expressions is elicited (Kiss & Eimer, 2008; Smith, 2012). This positivity originates in the prefrontal or anterior cingulate cortex and indicates the rapid detection of emotionally salient information (Eimer & Holmes, 2007). Taken together, emotional faces trigger a fast recruitment of attentional resources irrespective of conscious perception. However, only consciously perceived faces involve an additional, more elaborate structural analysis of the perceived facial information. While common and distinct brain processes in conscious emotion perception and emotion perception irrespective of conscious awareness have been identified in adults, it is not known whether comparable processes can be observed in infancy.

Prior work with infants has exclusively focused on the conscious processing of emotional facial expressions. Newborns show a basic preference for positive facial expressions (Farroni, Menon, Rigato, & Johnson, 2007). However, only from around 7 months of age, infants reliably distinguish between positive and negative emotions (Grossmann et al., 2011; Grossmann, Striano, & Friederici, 2007; Kobiella, Grossmann, Reid, & Striano, 2008; Leppänen, Moulson, Vogel-Farley, & Nelson, 2007; Peltola, Leppänen, Mäki, & Hietanen, 2009). In particular, previous infant ERP studies have revealed differences between emotional expressions for the negative component (Nc) (Grossmann et al., 2011; Hoehl & Striano, 2010; Leppänen et al., 2007; Nelson & de Haan, 1996). At 7 months, infants respond with a larger Nc to fearful compared to happy facial expressions and they look longer at fearful compared to happy facial expressions (Peltola et al., 2009). They also show differential responses to different negative facial expressions, as indicated by a larger Nc to angry compared to fearful facial expressions (Kobiella et al., 2008). These Nc differences suggest a differential allocation of attentional resources to emotional faces (Courchesne, Ganz, & Norcia, 1981; Richards, 2003; Webb, Long, & Nelson, 2005). In addition, differential responses to emotional faces can be observed for the N290/P400 complex (Hoehl & Striano, 2008; Kobiella et al., 2008; Leppänen et al., 2007). However, while some authors report a larger P400 for fearful facial compared to neutral facial expressions (Leppänen et al., 2007), others did not find any emotion effects at this component (Grossmann et al., 2007). Likewise for the N290, where some studies report differential responses to different emotional faces (Hoehl & Striano, 2008), while others did not observe emotion effects (Leppänen et al., 2007). Generally, both N290 and P400 have been link to the structural encoding and analysis of faces. In fact, the N290/P400 complex has been suggested as a precursor to the face-sensitive adult N170 (de Haan, Johnson, & Halit, 2003; de Haan, Pascalis, & Johnson, 2002; Halit, de Haan, & Johnson, 2003). Furthermore, differential processing of happy and fearful facial expressions has also been observed at the positivity before (Pb) (Nelson & de Haan, 1996; Grossmann et al., 2011). In sum, at around 7 months of age the brain processes that underlie the conscious perception of emotional facial expressions in infants are comparable to those in adults. Infants similarly display indices of increased attention as well as a more detailed structural analysis of the face in response to negative emotions, and in particular, fear. The lack of a fear bias in younger infants is thought to serve important adaptive functions related to bonding with a caregiver by increasing approach and reducing fear behaviors (Tottenham, 2012). Interestingly, the development of this fear bias also coincides with other crucial steps in development, including the emergence of stranger anxiety and locomotion (Campos, Kermoian, & Zumbahlen, 1992; Leppänen & Nelson, 2012). On a neural level, this development has been linked to a maturation of the amygdala and connected brain structures (see Tottenham, 2012, for a discussion). The question that remains is whether the brain processes underlying emotion processing can also be elicited when emotional faces are presented subliminally, and are therefore independent of conscious perception.

One crucial aspect in the investigation of unconscious emotion processing is to ensure that the emotional information is indeed subliminal, that is, not perceived consciously (see Wiens, 2006). Only recently have researchers begun to investigate the threshold for conscious perception in infants of different age groups. There is now behavioral evidence for such thresholds, suggesting that at 10 months of age, infants can only detect faces when presented for 150 msec or longer (Gelskov & Kouider, 2010). This indicates that the perceptual threshold for detecting faces in infants is approximately three times the duration in adults (e.g., Del Cul, Baillet, & Dehaene, 2007). This behavioral evidence is corroborated by ERP evidence identifying the late slow wave (LSW) as a neural marker for perceptual consciousness in infants (Kouider et al., 2013), which is evoked only when faces are presented above the perceptual threshold for a given age group. This work established that as a group, infants younger than 10 months of age do not consciously perceive information that is presented for less than 150 msec.

However, it has been shown in adults that the perceptual threshold for the detection of facial expressions varies considerably between individuals, which is an issue that has