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Neural processing of fearful and happy facial expressions during emotion-relevant and emotion-irrelevant tasks: A fixation-to-feature approach

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ABSTRACT

Research suggests an important role of the eyes and mouth for discriminating facial expressions of emotion. A gaze-contingent procedure was used to test the impact of fixation to facial features on the neural response to fearful, happy and neutral facial expressions in an emotion discrimination (Exp.1) and an oddball detection (Exp.2) task. The N170 was the only eye-sensitive ERP component, and this sensitivity did not vary across facial expressions. In both tasks, compared to neutral faces, responses to happy expressions were seen as early as 100–120 ms occipitally, while responses to fearful expressions started around 150 ms, on or after the N170, at both occipital and lateral-posterior sites. Analyses of scalp topographies revealed different distributions of these two emotion effects across most of the epoch. Emotion processing interacted with fixation location at different times between tasks. Results suggest a role of both the eyes and mouth in the neural processing of fearful expressions and of the mouth in the processing of happy expressions, before 350 ms.

1. Introduction

Facial expressions of emotion (hereafter facial emotions or facial expressions) are particularly salient stimuli and are direct indicators of others' affective dispositions and intentions (Adolphs, 2003). The ability to quickly extract facial information and discriminate between facial emotions is crucial for proper social communication (e.g., discerning a friend from foe; Mehrabian, 1968) and the neural correlates of these cognitive processes have been studied extensively using various neuroimaging techniques. Scalp Event Related Potentials (ERPs) are well suited to study the temporal dynamics of neuro-cognitive events and have been used to examine the time course of facial expression processing. However, results remain inconsistent (Rellecke, Sommer, & Schacht, 2013; and see Vuilleumier & Pourtois, 2007, for a review).

1.1. Early event-related potentials in facial expression research

The first visual ERP investigated in facial emotion research is the visual P1, (~80–120 ms post-stimulus onset at occipital sites), a component known to be sensitive to attention (Luck, 1995; Luck, Woodman, & Vogek, 2000; Mangun, 1995) and low-level stimulus properties such as color, contrast and luminance (Johannes, Münte, Heinze, & Mangun, 1995; Rossion & Jacques, 2008, 2012). A growing number of studies have now reported enhanced P1 amplitude for fearful relative to neutral faces (e.g., Batty & Taylor, 2003; Pourtois, Grandjean, Sander, & Vuilleumier, 2004; Sato, Kochiyama, Yoshikawa & Matsumura, 2001; Smith, Weinberg, Moran, & Jajcak, 2013; Wijers & Banis, 2012). It has been suggested that early occipito-temporal visual areas could be activated to a larger extent by intrinsically salient, threat-related stimuli, via possible projections from a subcortical route involving the amygdala (Vuilleumier & Pourtois, 2007). Fearful faces would automatically engage this subcortical structure which, in turn, would modulate and enhance cortical processing of the face stimuli (Morris et al., 1998; Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004; Whalen et al., 1998). Because of P1 early timing, which corresponds to the activation of early extrastriate visual areas (e.g., V2, V3, posterior fusiform gyrus, e.g., Clark, Fan, & Hillyard, 1995), this P1 fear effect is thought to reflect a coarse emotion extraction, the "threat gist" (e.g., Luo, Feng, He, Wang, & Lu, 2010; Vuilleumier & Pourtois, 2007), that might rely on fast extraction of low spatial frequencies (Vuilleumier, Armony, Driver, & Dolan, 2003). Actual processing of the visual threat would occur later, around or after the N170 (e.g., Luo et al., 2010), the second ERP component studied

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in facial expression research. However, let's note that this early P1 modulation by emotion is debated as many studies also failed to report modulations of the P1 by facial expressions of emotion (see Vuilleumier & Pourtois, 2007 for a review).

The N170 is a negative-going face-sensitive component measured at lateral occipito-temporal electrodes ~130–200 ms post stimulus onset, and is considered to index the structural processing of the face, i.e. a stage where features are integrated into the whole percept of a face (Bentin & Deouell, 2000; Bentin, Allison, Puce, Perez, & McCarthy, 1996; Itier & Taylor, 2002; Rossion et al., 2000). Studies have suggested the involvement of the fusiform gyrus (e.g., Itier & Taylor, 2002; Rossion et al., 1999), the Superior Temporal Sulcus (e.g., Itier & Taylor, 2004) and the Inferior Occipital Gyrus, or their combination, as potential generators of the N170 (for a review see Rossion & Jacques, 2012). Reports of the N170 sensitivity to facial emotions have been inconsistent. A number of studies have reported emotion effects with larger N170 recorded in response to emotional faces, especially fearful expressions, compared to neutral faces (e.g., Batty & Taylor, 2003; Blau, Maurer, Tottenham, & McCandliss, 2007; Caharel, Courtay, Bernard, & Lalonde, 2005; Leppänen, Hietanen, & Koskinen, 2008; Leppänen, Moulson, Vogel-Farley, & Nelson, 2007; also see Hinojosa, Mercado, & Carretié, 2015). However, as seen for the P1, a lack of sensitivity to facial expressions of emotion has also been reported for the N170 component in many studies (e.g., Ashley, Vuilleumier, & Swick, 2004; Balconi & Lucchiari, 2005; Herrmann et al., 2002; Krolak-Salmon, Fischer, Vighetto, & Mauguière, 2001; Münte et al., 1998; Pourtois, Dan, Grandjean, Sander, & Vuilleumier, 2005; Schupp, Junghöfer, Weike, & Hamm, 2004; Smith et al., 2013). Therefore it remains unclear whether facial expression processing, in particular that of fearful faces, interacts with the processing of the face structure, as indexed by the N170.

Another well studied ERP in facial expression research is the well-known marker of emotion processing Early Posterior Negativity (EPN), a negative deflection measured over temporo-occipital sites ~150–350 ms post-stimulus onset. The EPN is enhanced for emotional relative to neutral stimuli, for both verbal and non-verbal material including faces (Schacht & Sommer, 2009; Schupp, Markus, Weike, & Hamm, 2003; Schupp et al., 2004; Rellecke et al., 2013). Like the N170, the EPN is commonly reported to be most pronounced for threat-related expressions (i.e., fearful and angry) compared to neutral and happy expressions (e.g., Schupp et al., 2004; Rellecke, Palazova, Sommer, & Schacht, 2011), although there are reports of a general emotion effect with more negative amplitudes for both threatening and happy expressions compared to neutral expressions (Sato et al., 2001; Schupp, Flaisch, Stockburger, & Junghöfer, 2006). Therefore this effect has been suggested to reflect enhanced processing of emotionally salient faces in general or of threatening faces in particular (i.e., fearful and angry) in temporo-occipital areas possibly including occipital gyrus, fusiform gyrus and Superior Temporal Sulcus regions (Schupp et al., 2004). The current view is that the EPN reflects more in depth appraisal of the emotion, some form of semantic stage where the meaning of the emotion is extracted (Luo et al., 2010; Vuilleumier & Pourtois, 2007). Some studies have suggested that the EPN reflects the neural activity related to the processing of the emotion that is superimposed onto the normal processing of the face. This superimposed activity would sometimes start around the N170 and be responsible for the emotional effects reported for the N170 (Leppänen et al., 2008; Rellecke et al., 2011, 2013; Schupp et al., 2004), although it seems largest *after* the N170 peak and around the visual P2 (see Neath & Itier, 2015, for a recent example). In other words, the emotion effect on the N170 would actually reflect superimposed EPN activity (Rellecke et al., 2011; Rellecke, Sommer, & Schacht, 2012; Schacht & Sommer, 2009). According to this interpretation, face structural encoding, as indexed by the N170, and facial emotion encoding, do not really interact and are separate processes that occur independently and in parallel, as proposed by classic cognitive and neural models of face processing (Bruce & Young, 1986; Haxby, Hoffman, & Gobbini, 2000).

1.2. Role of facial features in the processing of facial expression

One factor possibly contributing to these inconsistent early ERP effects of emotion is the differing amount of attention to facial features. Some features characterize particular facial expressions better than others, like the smiling mouth for happy faces and the wide open eyes for fearful faces (e.g., Kohler et al., 2004; Leppänen & Hietanen, 2007; Nusseck, Cunningham, Wallraven, & Bülthoff, 2008; Smith, Cottrell, Gosselin, & Schyns, 2005). Behavioural research presenting face parts (e.g., Calder, Young, Keane, & Dean, 2000) or using response classification techniques such as *Bubbles* (e.g., Blais, Roy, Fiset, Arguin, & Gosselin, 2012; Smith et al., 2005) has highlighted the importance of these so-called "diagnostic features" for the discrimination and categorization of these facial emotions. Eye-tracking research also supports the idea that attention is drawn to these features early on, as revealed by spontaneous saccades towards the eyes of fearful faces or the mouth of happy faces presented for as short as 150 ms (Gamer, Schmitz, Tittgemeyer, & Schilbach, 2013; Scheller, Büchel, & Gamer, 2012).

The role of these diagnostic features in the neural response to facial expressions has recently been investigated in ERP research but remains unclear. Research using the *Bubbles* technique in combination with ERP recordings has suggested that the eye region provides the most useful diagnostic information for the discrimination of fearful facial expressions and the mouth for the discrimination of happy facial expressions, and that the N170 peaks when these diagnostic features are encoded (Schyns, Petro, & Smith, 2007, 2009). Leppänen et al. (2008) reported that an early fear effect, seen as more negative amplitudes for fearful compared to neutral faces from the peak of the N170 (~160 ms in that study) until 260 ms (encompassing the visual P2 and EPN), was eliminated when the eye region was covered, demonstrating the importance of this facial area in the neural response to fearful expressions. Calvo and Beltrán (2014) reported hemispheric differences in the processing of facial expressions using face parts and whole faces. An enhanced N170 in the left hemisphere was seen for happy compared to angry, surprised and neutral faces for the bottom face region presented in isolation (including the mouth), but not for the top face region presented in isolation (including the eyes), or for the presentation of the whole face. In the right hemisphere in contrast, the N170 was enhanced for angry compared to happy, surprised and neutral faces for whole faces only.

Taken together these studies suggest that the expression-specific diagnostic features modulate the neural response to facial expression at the level of the N170 or later. Importantly, all these ERP studies have employed techniques that forced feature-based processing by revealing facial information through apertures of various sizes and spatial frequencies (e.g. *Bubbles*, Schyns et al., 2007, 2009), by presenting isolated face parts (Calvo & Beltrán, 2014; Leppänen et al., 2008) or by covering portions of the face (Leppänen et al., 2008). However the bulk of the literature on face perception supports the idea that faces are processed holistically, i.e., as a whole, whether the focus is on identity (McKone, 2008; Rossion & Jacques, 2008) or emotion (Calder & Jansen, 2005; Calder et al., 2000) recognition. Moreover, components such as the N170 are very sensitive to disruption of this holistic processing (Rossion & Jacques, 2012; Itier, 2015, for reviews). A systematic investigation of the impact of facial features on the neural processing of facial emotion in the context of the whole face is lacking. This is important given we almost invariably encounter whole faces in our daily social interactions, and eye tracking studies suggest that faces are