On dissociating the neural time course of the processing of positive emotions

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ABSTRACT

Providing evidence for categorical theories of emotion mandates the inclusion of discrete emotion categories beyond the typical six "basic" emotions. Traditional neurophysiological investigations of emotion typically feature the six basic emotions with happiness as the lone positive exemplar. Here we studied how event-related potentials (ERPs) might differentiate between two positive emotional expressions: happiness and pride, and if so, at what time interval. Furthermore, given divergent findings in the ERP literature with respect to viewing emotional expressions, we explicitly examined how task type modulates neurophysiological responses when the same stimuli are viewed. While a continuous electroencephalogram (EEG) was recorded, 20 healthy participants completed two tasks: an *implicit* task where participants judged whether or not a face featured a brown spot (freckle), and an *explicit* task where they judged the face as portraying a "happy," "proud," or "neutral" expression. Behavioral performance exceeded 90% accuracy on both tasks. In the explicit task, participants responded faster and more accurately for Happy compared to Proud and Neutral expressions. Neurophysiologically, amplitudes for N170, VPP and P250 ERPs differentiated emotional from neutral expressions, but not from each other. In contrast, the late SPW component significantly differentiated Happy and Proud expressions from each other. Moreover, main effects of Task were found for the VPP, P250, LPP and SPW; additionally, Emotion X Task interactions were observed for P250 and SPW. Our data stress that task demands may magnify or diminish neural processing differences between emotion categories, which therefore cannot be disentangled with a single experimental paradigm. Additionally, some ERP differences may also reflect variations in categorization difficulty.

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1. Introduction

Whether emotions constitute discrete categories (Colombetti, 2009) such as anger and happiness, or are better decomposed into dimensional elements such as arousal and valence (Barrett et al., 2009) have been long debated among behavioral researchers studying emotions, as well as those studying the neural correlates of emotions (see Hamann, 2012; Lindquist et al., 2012). One of the ongoing challenges for discrete emotion theories in cognitive/social neuroscience is delineating to what extent emotions can be spatially and temporally isolated in the brain. Over the years studies using PET and fMRI have mapped selected neural regions that are typically the most responsive when perceiving other's emotional expressions (e.g. Blair et al., 1999; Kesler-West et al., 2001), and to a lesser extent when experiencing emotions oneself (e.g.

Kassam et al., 2013). When looked at as a whole, irrespective of emotion type, emotional face perception involves a distributed subset of regions from "social brain" networks, namely the amygdala, and orbitofrontal and occipito-temporal cortices (Adolphs, 2002; Aggleton, 1993; Rolls and Grabenhorst, 2008; Stanley and Adolphs, 2013). These regions have been found to be functionally and structurally connected to each other (Iidaka et al., 2001; Kim et al., 2011) and these connections are also formed early in life (see Leppänen and Nelson, 2009).

Meta-analyses of brain activations during emotion perception have found strong spatial correspondence between some specific emotions and particular brain regions: for example, fear and the amygdala (Fusar-Poli et al., 2009), and the subcallosal cingulate cortex and sadness (Phan et al., 2002). Beyond the spatial attributes of these activations, studies of the functional connectivity between brain regions find preliminary evidence for distinct couplings between regions for several emotions, particularly fear, disgust and happiness (see Tettamanti et al., 2012). In contrast, others have reported minimal evidence for specific neural

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correspondences by emotion, instead finding key regions such as the amygdala activate to emotional stimuli in general, regardless of category (e.g. Costafreda et al., 2008) and a large interactive set of brain regions that activate in response to all viewed emotions (see Lindquist et al., 2012). These conflicting results raise often asked questions about the roles that task requirements and top-down/bottom-up attentional processes might play in generating brain activation to viewed emotions (Palermo and Rhodes, 2007; Pessoa et al., 2002; Pessoa, 2005; Vuilleumier, 2005).

1.1. Temporal behavior of emotion processing as assessed by neurophysiology

The hemodynamic response is a proxy for neural activity, and reflects aggregated activation in a given brain region across a period of time. Changes in local field potential (Puce et al., 1997) or oscillatory activity (Engell et al., 2012) at different post-stimulus times could potentially contribute to the hemodynamic signal from one region. In contrast, the temporal dynamics underlying emotion processing can be disentangled using high-temporal resolution methods such as electroencephalography (EEG) and magnetoencephalography (MEG). In particular, there is an extensive literature investigating event-related potentials (ERPs) to viewing emotion categories (Eimer and Holmes, 2007; Hajcak et al., 2010; Schupp et al., 2006). ERPs are small, but time-locked, reproducible changes in neurophysiological activity that can be generated to external sensory or internally-generated cognitive or motor events. This millisecond temporal resolution is especially advantageous for linking behavior and brain in social cognition (Amodio et al., 2014), where behaviors unfold in stages over time and recruit both bottom-up and top-down mechanisms (see Ibanez et al., 2012, for a review).

Different ERP components have been reported to be preferentially sensitive to different emotional facial expressions (in Table 1 we summarize some of the more relevant studies.) However, overall there is mixed evidence regarding whether or not emotions modulate early visual components, including the P100, N170, the vertex positive potential (VPP), and the P250 (see Eimer and Holmes, 2007, for a review). The P100, also known as P1, peaks typically at around 100 ms over the occipito-temporal and occipito-parietal scalp, and can be larger for both fearful (e.g. Eimer and Holmes, 2002; Luo et al., 2010; Smith et al., 2013; Williams et al., 2006) and happy expressions (Dubal et al., 2011; Klucharev and Sams, 2004).

P100 is believed to reflect automatic visual processing of stimuli in an exogenous, stimulus-driven manner (Herrmann and Knight, 2001). The P100 has been linked to attentional orientation, as evidenced by larger responses for attended to compared to non-attended to locations and stimuli (Hillyard et al., 1973; Luck et al., 2000; Rugg et al., 1987; Taylor, 2002) particularly for threatening stimuli (Pourtois and Vuilleumier, 2006). Source localization studies have indicated that the lateral extrastriate cortex is the neural source for the P100 for these types of studies (Clark and Hillyard, 1996; Mangun et al., 1997), although P100 can also be locally generated within striate cortex for other types of tasks as shown by intracranial recordings in humans (Allison et al., 1999). Accordingly, the early P100 enhancement to happiness and fear suggests that these emotions may carry affective significance (Balconi and Pozzoli, 2003). Alternatively, low-level features such as changes in luminance and global/local contrast are also known to modulate P100 amplitude and latency (Chiappa, 1983; Halliday et al., 1973; Johannes et al., 1995; Puce et al., 2013; Regan, 1972). Hence, P100 enhancements to fearful and happy expressions may thus reflect differences in luminance and brightness, potentially from open mouths and exposed teeth. Realistically, it is likely that multiple mechanisms might modulate P100 amplitude and latency

for these complex stimuli. Practically, if there are multiple processes that contribute to P100 modulation (or modulation of other ERPs), one way to disentangle these would be to run a series of different task and stimulus manipulations in the same participants.

A vast literature also exists for the N170 – the ERP component that follows P100. N170 is a negative-going ERP component at around 170 ms that is maximal over the occipito-temporal scalp. N170 amplitude is consistently larger for faces compared to other visual stimuli (e.g. objects; see Bentin et al., 1996; Itier and Batty, 2009; Rossion and Jacques, 2008), leading researchers to conclude it is a signal of the "perceptual awareness" of a face (see Rossion, 2014). N170 amplitude can differentiate between emotional and neutral expressions (e.g. Calvo and Beltrán, 2014; Wronka and Walentowska, 2011), though modulations for particular emotions such as fear (Batty and Taylor, 2003; Williams, 2006) and anger (e.g. Calvo and Beltrán, 2013; Krombholz et al., 2007; Rellecke et al., 2013) have been observed (see Hinojosa et al., 2015 for a meta-analysis). However, other studies have failed to find any modulation of the N170 amplitude by emotion (e.g. Ashley et al., 2004; Eimer et al., 2003), so the functional significance of the N170 with respect to the processing of facial emotional expressions remains to be clarified.

A positive-going vertex maximal component that occurs in the same time window as N170 – the vertex positive potential (VPP) – is similarly responsive to faces (Jeffreys, 1989; Jeffreys and Tukmachi, 1992). The VPP can be enhanced for fearful (Williams et al., 2006) and happy expressions (Luo et al., 2010) compared to neutral, however; as for N170, other studies have failed to find these differences as a function of emotion (e.g. Herrmann et al., 2002; Rossignol et al., 2005).

Following the N170/VPP, also maximal at occipito-temporal sites, is the P250. The P250 is responsive to emotional information: amplitudes are augmented for emotional expressions compared to neutral (Chang et al., 2010), as with the N170 (Hinojosa et al., 2015). These modulations may be driven by stimulus salience, as larger P250 amplitudes are found for fearful expressions with enlarged eye white area (Feng et al., 2009). P250 amplitude can be also mitigated by familiarity, with more familiar faces eliciting smaller amplitudes (Caharel et al., 2007). Following P250, an inflexion in the ERP waveform known as the early posterior negativity (EPN) can occur between 200 and 300 ms post-stimulus. Its amplitude can differ between emotional and neutral expressions (e.g. Debruille et al., 2011; Sato et al., 2001; Wronka and Walentowska, 2011), for emotions such as happiness (Rellecke et al., 2012), anger (Calvo and Beltrán, 2013, 2014; Rellecke et al., 2012), and to a lesser extent fear and sadness (e.g. Smith et al., 2013).

Lastly, two later ERP components – the late positive potential (LPP) and the slow positive wave (SPW) – have been reported to be sensitive to viewing emotional expressions. The LPP is usually seen at central midline sites during a time interval of 400–700 ms, but can extend to parietal sites as well, and is enhanced for more arousing stimuli, regardless of valence (Olofsson et al., 2008; Schupp et al., 2000). This enhancement potentially reflects motivational processing (see Ibanez et al., 2012) that is the product of both bottom-up perceptual processes and top-down cognitive control (Moratti et al., 2011). The SPW follows the LPP (> 700 ms) and is maximal over centro-parietal sites; a recent study found larger SPWs for ambiguous expressions compared to non-ambiguous expressions (Debruille et al., 2011), potentially reflecting categorization and response selection processes (Calvo and Beltrán, 2013).

1.2. Can differences in task demands explain the variability in the literature?

Why are there such disparities in the literature related to