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Visual adaptation provides objective electrophysiological evidence of facial identity discrimination

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ABSTRACT

Discrimination of facial identities is a fundamental function of the human brain that is challenging to examine with macroscopic measurements of neural activity, such as those obtained with functional magnetic resonance imaging (fMRI) and electroencephalography (EEG). Although visual adaptation or repetition suppression (RS) stimulation paradigms have been successfully implemented to this end with such recording techniques, objective evidence of an identity-specific discrimination response due to adaptation at the level of the visual representation is lacking. Here, we addressed this issue with fast periodic visual stimulation (FPVS) and EEG recording combined with a symmetry/asymmetry adaptation paradigm. Adaptation to one facial identity is induced through repeated presentation of that identity at a rate of 6 images per second (6 Hz) over 10 sec. Subsequently, this identity is presented in alternation with another facial identity (i.e., its anti-face, both faces being equidistant from an average face), producing an identity repetition rate of 3 Hz over a 20 sec testing sequence. A clear EEG response at 3 Hz is observed over the right occipito-temporal (ROT) cortex, indexing discrimination between the two facial identities in the absence of an explicit behavioral discrimination measure. This face identity discrimination occurs immediately after adaptation and disappears rapidly within 20 sec. Importantly, this 3 Hz response is not observed in a control condition without the single-identity 10 sec adaptation period. These results indicate that visual adaptation to a given facial identity produces an objective (i.e., at a pre-defined stimulation frequency) electrophysiological index of visual discrimination between that identity and another, and provides a unique behavior-free quantification of the effect of visual adaptation.

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1. Introduction

The discrimination of facial identities serves as an important function for human social life and reflects the remarkable ability of the human visual system to distinguish between different exemplars within a category. This ability is especially impressive when considering that the physical differences between facial identities may be subtle and in the natural environment are often presented in tandem with dramatic differences in viewing conditions, e.g., luminance, direction of the lighting source, viewing angle, etc.

Despite the challenges in detecting relevant visual differences between facial identities and connecting such visual information to specific representations of these identities, humans are capable of discriminating images of facial identities rapidly and accurately (e.g., Jacques, d'Arripe, & Rossion, 2007). Further evidence that this function is specialized in the human brain comes from stimulus manipulations that uniquely affect discrimination of facial identities compared to discrimination within other object categories, e.g., the face inversion effect (Busigny & Rossion, 2010; Robbins & McKone, 2007; Rossion, 2008; Sergent, 1984; Valentine & Bruce, 1986; Yin, 1969 for review). Indeed, human face perception is known to implicate a complex, distributed network along the ventral surface of the occipito-temporal cortex with a right hemisphere advantage (e.g., Haxby, Hoffman, & Gobbini, 2000; Puce, Allison, Gore, & McCarthy, 1995; Rossion, Alonso-Prieto, Boremanse, Kuefner, & Van Belle, 2012; Rossion, Hanseeuw, & Dricot 2012; Sergent, Ohta, & MacDonald, 1992; Weiner & Grill-Spector, 2010; Zhen et al., 2015).

However, studying facial identity discrimination at a neural level has been challenging because measurements of macroscopic neural activity, such as those obtained with functional magnetic resonance imaging (fMRI), or electroencephalography (EEG), are not inherently sensitive to differences in facial identity. This is likely due to the level of organization at which face identity is coded in the brain. Recordings from macaque monkeys in the infero-temporal (IT) cortex have found single neurons that differentiate individual (human and monkey) facial identities, these neurons discharging at a different rates to pictures of different faces (e.g., Freiwald, Tsao, & Livingstone, 2009; Leopold, Bondar, & Giese, 2006; Rolls, 2001; Rolls, Aggelopoulos, Franco, & Treves, 2004; Young & Yamane, 1992). This has inspired the view that facial identities are coded for sparsely, i.e., within a small population of neurons. Therefore, if different facial identities are coded for with overlapping representations in a distributed neural population, differences in responses to facial identities may be revealed only at a very fine scale and may not be reflected in overall changes at the level of the population (Meyers, Borzello, Freiwald, & Tsao, 2015).

In humans, patterns of activity within regions have been used to examine finer-grained activations in fMRI [e.g., multivariate pattern analysis (MVPA); Kriegeskorte, Formisano, Sorger, & Goebel, 2007; Norman, Polyn, Detre, & Haxby, 2006]. However, approaches such as MVPA rely on the scale available from the voxel-resolution of fMRI (i.e., several cubic millimeters, an area containing millions of neurons), and there is no evidence that facial identity is coded on a

corresponding scale. Hence, MVPA-fMRI has generally failed to decode (i.e., discriminate) face identity in cortical face-selective regions of the human brain (e.g., Kriegeskorte et al., 2007; Natu et al., 2010) or to provide evidence that such decoding is not based on low-level image cues differentiating a few items, without much reliability and consistency across studies (e.g., Gosaert & Op de Beeck, 2013; Nestor, Plaut, & Behrmann, 2011; see the discussion in Rossion, 2014; Dubois, de Berker, & Tsao, 2015; see however Davidesco et al., 2014 for discrimination of photographs of vastly different face identities in local field potential responses on the cortical surface). Given the limited spatial resolution of the technique, there is even less reason to expect that MVPA applied to EEG data measured on the scalp would be able to reliably distinguish neural responses to different facial identities.

Combining a visual paradigm of adaptation or repetition suppression (RS), namely, the reduction of neural activity following repetition of the same stimulus, to techniques such as fMRI and EEG has offered a reliable means to distinguish between neural representations of facial identities in the human brain. In humans, RS has been used from its first application with fMRI (fMR-A, Grill-Spector et al., 1999; Grill-Spector & Malach, 2001; Henson & Rugg, 2003) to define the regions subtending individual face discrimination (e.g., Andrews & Ewbank, 2004; Gauthier et al., 2000; Gentile & Rossion, 2014; Harris, Young, & Andrew, 2014) and characterize the nature of individual face discrimination in these regions (i.e., which properties or processes subtend individual face discrimination; see e.g., Andrews, Davies-Thompson, Kingstone, & Young, 2010; Davies-Thompson, Gouws, & Andrews, 2009; Ewbank & Andrews, 2008; Ewbank, Henson, Rowe, Stoyanova, & Calder, 2013; Goffaux, Schiltz, Mur, & Goebel, 2012; Grotheer, Hermann, Vidnyánszky, & Kovács, 2014; Jiang, Dricot, Blanz, Goebel, & Rossion, 2009; Schiltz & Rossion, 2006; Yovel & Kanwisher, 2005; Winston, Henson, Fine-Goulden, & Dolan, 2004).

Facial identity adaptation has also been used with human electrophysiology at the population level, i.e., EEG recorded on the scalp (see Engell & McCarthy, 2014, for evidence of RS of facial identity in electrocorticography). For instance, the N170, a negative component observed on occipito-temporal sites that is particularly large when evoked by faces (Bentin, McCarthy, Perez, Puce, & Allison, 1996; Rossion & Jacques, 2011 for review) is reduced in amplitude following the immediate repetition of a facial identity (e.g., Caharel, d'Arripe, Ramon, Jacques, & Rossion, 2009; Caharel, Collet, & Rossion, 2015; Caharel, Jiang, Blanz, & Rossion, 2009; Itier & Taylor, 2002; Heisz, Watter, & Shedden, 2006; Jacques et al., 2007). However, amplitude reduction of the N170 following face identity repetition is a relatively small effect compared to the overall amplitude of the N170, and may depend on specific stimulation parameters (i.e., immediate repetition, short interstimulus interval, long duration the face adapter; see Rossion & Jacques, 2011 for discussion). Therefore, the N170 adaptation effect requires many trials to reach statistical significance, and is not found systematically (e.g., Amihai, Deouell, & Bentin, 2012; Bindemann, Burton, Leuthold, & Schweinberger, 2008; Schweinberger, Pickering, Jentsch, Burton, & Kaufmann,

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