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An objective index of individual face discrimination in the right occipito-temporal cortex by means of fast periodic oddball stimulation

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ABSTRACT

We introduce an approach based on fast periodic oddball stimulation that provides objective, high signal-to-noise ratio (SNR), and behavior-free measures of the human brain's discriminative response to complex visual patterns. High-density electroencephalogram (EEG) was recorded for human observers presented with 60 s sequences containing a base-face (A) sinusoidally contrast-modulated at a frequency of 5.88 Hz (F), with face size varying every cycle. Different oddball-faces (B, C, D…) were introduced at fixed intervals (every 4 stimuli $= F/5 = 1.18$ Hz: AAAABAAAACAAAAD…). Individual face discrimination was indexed by responses at this 1.18 Hz oddball frequency. Following only 4 min of recording, significant responses emerged at exactly 1.18 Hz and its harmonics (e.g., $2F/5 = 2.35$ Hz, $3F/5 = 3.53$ Hz…), with up to a 300% signal increase over the right occipito-temporal cortex. This response was present in all participants, for both color and greyscale faces, providing a robust implicit neural measure of individual face discrimination. Face inversion or contrast-reversal did not affect the basic 5.88 Hz periodic response over medial occipital channels. However, these manipulations substantially reduced the 1.18 Hz oddball discrimination response over the right occipito-temporal region, indicating that this response reflects high-level processes that are partly face-specific. These observations indicate that fast periodic oddball stimulation can be used to rapidly and objectively characterize the discrimination of visual patterns and may become invaluable in characterizing this process in typical adult, developmental, and neuropsychological patient populations.

1. Introduction

One of the most fundamental and complex functions of the human brain is to discriminate between visually similar items in order to guide behavior. Our ability to differentiate people based on their faces illustrates the potential finesse of such discrimination. Despite the high similarity between faces, humans are extremely efficient at accomplishing this task. Behavioral studies have revealed which visual cues play an important role in individual face discrimination. For instance, the eye region is particularly diagnostic (Haig, 1985; Sadr, Jarudi, & Sinha, 2003), and at the global level of the face, shape and surface cues (e.g., texture, color) provide complementary information (Jiang, Blanz, & O'Toole, 2006; see Bruce & Young, 2012). Furthermore, there is evidence that facial features are not processed independently, but integrated into so-called "holistic/configural" representations, which facilitate individual face discrimination (Sergent, 1984;

Young, Hellawell, & Hay, 1987; Tanaka & Farah, 1993; Farah, Wilson, Drain, & Tanaka, 1998; Rossion, 2013). At the neural level, there is an entire neural network involved in individual face discrimination, with key areas located in the right ventral occipito-temporal cortex (Sergent, Ohta, & MacDonald, 1992; Gauthier et al., 2000; Grill-Spector et al., 1999; Andrews & Ewbank, 2004; Schiltz & Rossion, 2006; Gilae-Dotan & Malach, 2007; Davies-Thompson, Gouws, & Andrews, 2009; Xu & Biederman, 2010).

The true complexity of face discrimination is highlighted by the considerable inter-individual variance of this ability in the normal adult population (Bowles et al., 2009; Wilmer et al., 2010). Long-term deficits, in the absence of brain damage, seem to be more prevalent than initially thought (Behrmann & Avidan, 2005; Duchaine & Nakayama, 2006). Additionally, this function can be impaired by simple stimulus manipulations such as picture-plane inversion or contrast-reversal. These two manipulations dramatically reduce individual face discrimination performance (for inversion, see e.g., Yin, 1969; Freire, Lee, & Symons, 2000; for a review, see Rossion, 2009; for contrast-reversal, see e.g., Galper, 1970; Bruce & Langton, 1994; Russell, Sinha, Biederman, & Nederhouser,

2006; Russell, Biederman, Nederhouser, & Sinha, 2007). Humans are also poor at discriminating individual faces of a non-experienced morphology (e.g., the "other-race effect", Malpass & Kravitz, 1969; for review: Rossion & Michel, 2011, and the "other-age effect", Kuefner, Macchi Cassia, Picozzi, & Bricolo, 2008; Hills & Lewis, 2011; for a review: Rhodes & Anastasi, 2012). Individual face discrimination may be further impaired in neuropsychiatric disorders such as autism (Boucher & Lewis, 1992; Klin et al., 1999), or in the right variant of fronto-temporal dementia (e.g. Gainotti, Barbier, & Marra, 2003). In case of brain damage to right occipito-temporal areas leading to prosopagnosia, individual face discrimination can be severely and specifically disrupted (e.g., Hécaen & Angelergues, 1962; Barton, Cherkasova, Press, Intriligator, & O'Connor, 2004; Bouvier & Engel, 2006; Busigny, Graf, Mayer, & Rossion, 2010).

The importance of understanding individual face discrimination calls for an objective and highly sensitive discrimination measure, which could be recorded independently from behavioral performance and without contamination by irrelevant attentional and decisional processes. Such an approach was recently proposed in the form of electrophysiological (electroencephalogram, EEG) recordings on the scalp during fast periodic visual stimulation (e.g., Rossion & Boremanse, 2011), which results in steady-state visual evoked potentials (SSVEPs, Regan, 1966,1989). The principle is very simple: presenting stimuli at a fixed rate generates a periodic EEG response at exactly the same frequency. In recent studies, individual face discrimination was assessed with this method by presenting short sequences (i.e., 60 s) of same or different faces at a specific frequency (i.e., 4 Hz = 4 faces per second) through sinusoidal contrast modulation (Rossion & Boremanse, 2011; Rossion, Alonso Prieto, Boremanse, Kuefner, & Van Belle, 2012; Prieto, Van Belle, Liu-Shuang, Norcia, & Rossion, In press). In these studies, a robust EEG response at the stimulation frequency (i.e., 4 Hz in the EEG frequency spectrum) was larger when different faces were shown than when the same face was repeated, even though face identity was task-irrelevant (fixation-cross color change detection). This difference was the largest over the right occipito-temporal cortex and was significantly reduced following picture-plane inversion (Rossion & Boremanse, 2011; Rossion et al., 2012) and contrast-reversal (Rossion et al., 2012). The combination of its topography and the presence of face-specific effects indicate that this difference can be taken as an objective and sensitive index of individual face discrimination. The objectivity of this approach derives from the fact that the response is measured exactly at a predefined experimental frequency. Hence, responses at other frequencies in the EEG spectrum, even at neighboring frequencies, e.g., 3.8 Hz or 4.2 Hz, can be disregarded as noise (see Rossion & Boremanse, 2011, Rossion et al., 2012 for a more in-depth discussion of the advantages of the fast periodic visual stimulation approach in high-level vision).

The aim of the current study is to extend this previous work and to provide an improved, more efficient method to measure visual discrimination by using a *fast periodic oddball* paradigm. This method measures the discrimination between base and oddball stimuli, differing on a dimension of interest (e.g., orientation, color, shape…), that are presented at two different periodicities within the same sequence. For example, base stimuli, i.e., blue dots, are shown a constant rate (base frequency = F Hz), and oddball stimuli, i.e., red dots, are presented within the sequence of base stimuli at fixed intervals (oddball frequency = every n base stimuli or F/n Hz). Fast periodic visual stimulation is based on the assumption that a periodically presented stimulus will elicit a periodic EEG response only if this periodicity is detected by the brain. Hence, if the brain is able to differentiate base and oddball stimuli based on the manipulated dimension, i.e., blue vs. red, it would detect two periodicities (base frequency and oddball frequency) and generate two periodic responses at F Hz and F/n Hz, respectively. In contrast, if the brain does not discriminate the dimension of interest, it will produce only one

periodic response, at F Hz. Thus, the presence of a response at the oddball frequency directly reflects the discrimination of the base and oddball stimuli on the relevant dimension.

All the previous periodic face stimulation studies referred to above used a block design in which the two conditions of interest were recorded in different sequences (Rossion & Boremanse, 2011; Rossion et al., 2012; Prieto et al., In press). However, evaluating discrimination based on a "different–same" subtraction assumes that participants maintain the same level of attention/arousal to sequences of the exact same faces compared to those of different faces. This, of course, might not necessarily be the case and there is always a concern that noise could affect one condition more than the other. The periodic oddball approach may overcome this limitation by collapsing the "same" and "different" conditions within the same sequence. Discrimination is then indexed by the presence of a significant response at the oddball frequency, which encapsulates the "different–same" subtraction.

An additional aim of the current study is to test whether discrimination responses can be obtained for high-level stimuli and in the absence of explicit processing of the oddball stimuli. This approach based on periodic stimulation and two embedded frequency rates has been previously used to measure sensitivity to low-level visual properties in infants, such as orientation selectivity (Braddick, Wattam-Bell, & Atkinson, 1986; Braddick, Birtles, Wattam-Bell, & Atkinson, 2005) and motion direction selectivity (Braddick et al., 2005). More recently, two studies have used a similar logic in adults in the context of an oddball paradigm (orientation selectivity: Heinrich, Mell, & Bach, 2009; color: Hönegger et al., 2011). However, to the best of our knowledge, this approach has not been used to measure high-level visual processes, and in particular the discrimination of complex visual patterns such as faces. Moreover, in these latter two studies (Heinrich et al., 2009; Hönegger et al., 2011), participants were explicitly instructed to attend to the oddball stimuli.

In the present study, individual faces were sinusoidally contrast-modulated at a frequency of 5.88 Hz (base frequency F) for 60 s. This stimulation was expected to lead to a large EEG response confined to the 5.88 Hz stimulation frequency, reflecting the appearance of a face on the background (i.e., face onset; Prieto et al., In press). The same *base* face (A) was repeated throughout a sequence. Within this sequence, different *oddball* faces (B, C, D…) were introduced periodically, at a rate of every 5th base face, so at an oddball frequency of 1.18 Hz ($F/5 = 5.88$ Hz/5). A sequence was therefore structured as follows: AAAABAAAACAAAAD… We hypothesized that if individual faces were visually discriminated, there would be a periodic EEG response exactly at the frequency of the oddball faces, i.e., 1.18 Hz, in brain regions coding for individual faces (i.e., the occipito-temporal cortex). Since the actual waveform of the oddball stimulation is a square-wave with a duty cycle of 20%, we expected the EEG response to also contain harmonic frequencies of 1.18 Hz (i.e., integer multiples of 1.18 Hz: $2F/5 = 2.35$ Hz, $3F/5 = 3.53$ Hz…). In the frequency-domain, this would correspond to a peak in the EEG amplitude spectrum at exactly 1.18 Hz and its harmonics. Critically, in order to demonstrate that these oddball responses reflect high-level face processing, we manipulated face orientation (Experiment 1: upright vs. inverted) and contrast polarity (Experiment 2: normal contrast vs. contrast-reversed). Since these manipulations lead to face-specific discrimination impairments, we predicted that they would specifically reduce the 1.18 Hz oddball response over face-related regions.

2. Experiment 1: Upright vs. inverted faces

2.1. Materials and methods

2.1.1. Participants

Twelve participants (5 males, mean age = 24 ± 4, range = 19–37), all of whom gave written informed consent and received financial compensation for their participation, were tested in the experiment. The experimental and consenting