



The face evoked steady-state visual potentials are sensitive to the orientation, viewpoint, expression and configuration of the stimuli



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ABSTRACT

Previous studies demonstrated that the steady-state visual-evoked potential (SSVEP) is reduced to the repetition of the same identity face when compared with the presentation of different identities, suggesting high-level neural adaptation to face identity. Here we investigated whether the SSVEP is sensitive to the orientation, viewpoint, expression and configuration of faces (Experiment 1), and whether adaptation to identity at the level of the SSVEP is robust enough to generalize across these properties (Experiment 2). In Experiment 1, repeating the same identity face with continuously changing orientation, viewpoint or expression evoked a larger SSVEP than the repetition of an unchanged face, presumably reflecting a release of adaptation. A less robust effect was observed in the case of changes affecting face configuration. In Experiment 2, we found a similar release of adaptation for faces with changing orientation, viewpoint and configuration, as there was no difference between the SSVEP for the same and different identity faces. However, we found an adaptation effect for faces with changing expressions, suggesting that face identity coding, as reflected in the SSVEP, is largely independent of the emotion displayed by faces. Taken together, these results imply that the SSVEP taps high-level face representations which abstract away from the changeable aspects of the face and likely incorporate information about face configuration, but which are specific to the orientation and viewpoint of the face.

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1. Introduction

The peculiar nature of face representations in the human brain is a long-standing issue in cognitive neuroscience. Functional magnetic resonance imaging (fMRI) studies have identified several face-sensitive cortical areas that respond stronger to faces than to objects, such as the fusiform face area (FFA; Kanwisher et al., 1997; for a review, see Kanwisher and Yovel, 2006), the occipital face area (OFA; Gauthier et al., 2000; for a review, see Pitcher et al., 2011), and a posterior region of the superior temporal sulcus (STS; Engell and Haxby, 2007; Hoffman and Haxby, 2000; Narumoto et al., 2001) that constitute a cortical network dedicated to the processing of facial information (Gobbini and Haxby, 2007; Haxby et al., 2000, 2002; for a recent review, see Haxby and Gobbini, 2011). Electrophysiological studies have thoroughly analyzed the N170 component, a negative deflection of the event-related potential (ERP) peaking approximately 170 ms after stimulus onset, which is face-sensitive in the sense that it is higher in amplitude to

pictures of faces than to exemplars of several other non-face object categories (Bentin et al., 1996; for reviews, see Eimer, 2011; Rossion and Jacques, 2008, 2011).

One approach to unravel the neural representation of faces is to take advantage of the fact that neural activity is reduced when the same stimuli are repeated, as compared with the condition when novel stimuli are presented in succession. This phenomenon, termed as “repetition suppression” (RS) or “neural adaptation” (ADA), has been observed on the single-cell level (Baylis and Rolls, 1987; Desimone, 1996), and it is also evident in the attenuation of the ERP and of the fMRI responses to visual object repetition in humans, the latter termed as fMRI adaptation (fMRIa; for reviews, see Grill-Spector et al., 2006; Krekelberg et al., 2006). RS is of interest due to its potential to reveal the sensitivity of a neural population to various aspects of visual objects and faces (Grill-Spector et al., 1999; Grill-Spector and Malach, 2001). The logic behind the experiments exploiting this phenomenon is as follows. Given that the neural response attenuates during the repetition of the same stimulus, presumably reflecting ADA, an increase in the response (presumably reflecting a “release” of ADA) should be observed whenever a particular stimulus attribute or feature is changed, provided that the activity of the underlying neurons reflect the change of that feature. This release of ADA is expected if the altered stimulus activates a fresh, non-adapted subpopulation of neurons. On the other hand, the

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neural response is assumed to remain attenuated if the underlying neurons are insensitive to differences along the altered stimulus dimension (Grill-Spector and Malach, 2001).

In relation to face individuation, it has been shown that a change in facial identity between subsequently presented faces results in a release of ADA reflected in the BOLD signal in several regions of the cortical face processing network (Andrews and Ewbank, 2004; Eger et al., 2004; Ewbank and Andrews, 2008; Gauthier et al., 2000; Mazard et al., 2006; Winston et al., 2004). The amplitude of the N170 (Campanella et al., 2000; Guillaume and Tiberghien, 2001; Heisz et al., 2006a,b; Itier and Taylor, 2002; Jacques et al., 2007) and its neuromagnetic counterpart, the M170 (Ewbank et al., 2008) is larger in response to a face that is preceded by a different identity face when compared with the condition in which the same face is repeated (for different results, see e.g. Amihai et al., 2011; Schweinberger et al., 2002; see also Rossion and Jacques, 2011 for a review). These studies demonstrate the usefulness of ADA methods in gaining information about the spatial distribution and the time-course of activation of individual face representations in the human brain.

Recent studies have shown that ADA is also reflected in the reduction of the steady-state visual evoked potentials (SSVEPs) to repeated face stimuli (Rossion and Boremanse, 2011; Rossion et al., 2012). SSVEPs are oscillatory neuro-electric signals that arise in response to periodic stimulation of the visual system, and can be recorded from the human scalp with standard electroencephalographic (EEG) methods (Regan, 1966, 2009). In the frequency domain, these responses are characterized by a fundamental frequency, corresponding to the driving frequency of the stimulus train, and often a series of related harmonic frequencies. Rossion and Boremanse (2011) and Rossion et al. (2012) demonstrated that the continuous repetition of faces elicits a steady-state response at the corresponding fundamental frequency, and that this response is reduced when the same face is repeated, when compared with a condition in which different identity faces are presented in succession. This novel finding suggested that the face-evoked SSVEP reflects activity related to the neural mechanisms engaged in the individuation of faces, and that analyzing steady-state responses may provide further insight into how the human brain processes face-related information (Rossion and Boremanse, 2011).

Rossion and Boremanse (2011) highlights the advantages of the SSVEP approach over the more conventional ERP/fMRI methods used in face perception research. They argue that the SSVEP has a remarkably high signal to noise ratio, and the signal can be identified easily, as the response depends on the driving frequency of the stimulus train. Moreover, quantifying the magnitude of the response is less ambiguous than in the case of transient ERP components, such as the N170. To date, there is little evidence regarding the relationship between the face-evoked steady-state response and the face sensitive ERP components such as the N170. In the auditory domain, it has been shown that the 40 Hz auditory steady-state response (ASSR) can be explained by the temporal superposition of transient ERP components (Bohorquez and Ozdamar, 2008) and similar results have been obtained in the visual domain using relatively simple stimuli. Capilla et al. (2011) demonstrated that SSVEPs evoked by a reversing checkerboard stimulus can be explained by the summation of transient responses. The authors concluded that the same neural mechanism might be responsible for the generation of both the steady-state and transient event-related potentials. Taken together, these results suggest a linear relationship between transient and steady-state responses. On the other hand, the results of a more recent study investigating the modulation of the face-evoked steady-state response and the N170 by face inversion are not indicative of such a simple relationship (Gruss et al., 2012). While the authors found a linear relationship between the amplitude enhancement of the N170 and the SSVEP, such a relationship was present only at one of the four tested driving frequencies (20 Hz). In addition, preliminary results from the same laboratory involving computational modeling do not indicate that the SSVEP can be explained by the linear

superposition of the N170 responses (Gruss et al., 2012). Furthermore, it has been also argued previously that drawing parallels between the steady-state response and discrete ERP components is not straightforward. According to Rossion et al. (2012), the face-related SSVEP likely reflects high-level processes that contribute to the ERP components taking place below 250 ms (given a 4 Hz stimulation frequency) such as the N170, and also lower-level ones possibly related to the P1 component.

Regarding the adaptation characteristics of the face-evoked steady-state response, it has been shown that the ADA effect of the SSVEP signal (i.e., its reduction in magnitude to the repetition of the same face when compared with different faces) is reduced (Rossion et al., 2012) or even eliminated (Rossion and Boremanse, 2011) when the faces are turned upside-down. Perceptually, the detrimental effect of inversion on face recognition is disproportionately large when compared with the effect of inverting exemplars of non-face object categories, and hence this transformation is assumed to tap face-specific processing mechanisms (Yin, 1969). The effect of face inversion is thought to be the consequence of the difficulty in extracting the spatial relations among face elements (Diamond and Carey, 1986; Maurer et al., 2002), or the integration of face parts into a unified, holistic percept (Maurer et al., 2002; Rossion, 2008, 2009). Therefore, the lack of ADA of the SSVEP signal for inverted faces indicates that the face-evoked SSVEP reflects the activation of configural or holistic face representations (Maurer et al., 2002; Rossion and Boremanse, 2011; Tanaka and Farah, 1993; Young et al., 1987). This assumption is supported by more recent observations showing that SSVEP responses to whole-face configurations can be dissociated from responses to face parts (Boremanse et al., 2013, in press).

A recent study has shown that the reduction of the SSVEP to repeated identities is smaller for emotional faces when compared with faces with neutral expression, and that this reduction is more pronounced in the case of negative when compared with positive valence expressions (Gerlicher et al., 2014). Interestingly, the ADA effect in that study was confined to several medial occipital electrode sites, and this distribution is different from the cluster of right hemisphere occipito-temporal channels implicated in previous studies (Rossion and Boremanse, 2011; Rossion et al., 2012). It is not clear whether this discrepancy is attributable to the slightly different stimulation frequencies employed in these studies, or to other methodological factors.

Finally, the SSVEP ADA effect to repeated faces was also reduced when the contrast polarity of the faces is reversed (Rossion et al., 2012). This result is in line with the well-known detrimental effect of contrast reversal on face recognition (Galper, 1970; Galper and Hochberg, 1971). Taken together, these observations show that the face-evoked SSVEP is a valuable tool to investigate the nature of the neural representation of faces.

In the present study, our aim was to investigate further the functional properties of the face-evoked SSVEP in two ADA experiments. First, we aimed at replicating previous findings regarding SSVEP ADA to face identity by comparing the magnitude of the response between conditions in which the same face, or different identity faces are presented in succession (Rossion and Boremanse, 2011; Rossion et al., 2012). Second, we examined whether this SSVEP ADA is sensitive to manipulations which substantially alter the appearance of the face, but which nevertheless do not change face identity (Experiment 1). Third, and most importantly, we investigated whether face individuation, as reflected in the SSVEP, is invariant to changes in these properties (Experiment 2).

We applied four such stimulus manipulations. First, we varied the in-plane orientation of the stimuli. Face-selective cells in the macaque inferior temporal (IT) cortex and STS have been shown to tolerate substantial changes of face orientation in the picture plane (Desimone et al., 1984; Perrett et al., 1982, 1985; but see Tanaka et al., 1991), while in humans, several studies demonstrated a linear relationship between the degree of rotation from the upright orientation and the decrement in face recognition performance (Collishaw and Hole, 2002; Valentine and Bruce, 1988). On the other hand, deviations from linearity have

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