Neuroscience Letters 562 (2014) 19–23

Contents lists available at ScienceDirect

Neuroscience Letters

journal homepage: www.elsevier.com/locate/neulet

Steady-state visual-evoked response to upright and inverted geometrical faces: A magnetoencephalography study

Aki Tsuruhara[a,*], Koji Inui[a,b], Ryusuke Kakigi[a,b]

[a] *Department of Integrative Physiology, National Institute for Physiological Sciences, Okazaki 444-8585, Japan*
[b] *Department of Physiological Sciences, School of Life Sciences, The Graduate University for Advanced Studies, Hayama, Kanagawa 240-0193, Japan*

HIGHLIGHTS

- The face inversion effect on steady-state visual-evoked magnetic fields was studied.
- Upright and inverted faces elicited clear SSVEF responses.
- Face inversion delayed the latency of SSVEFs in the right temporal area.
- SSVEF amplitudes were not different between upright and inverted faces.
- Different systems may lie in the delayed and enhanced responses by face inversion.

ARTICLE INFO

Article history:
Received 26 August 2013
Received in revised form
19 December 2013
Accepted 2 January 2014

Keywords:
Magnetoencephalography
Steady-state visual-evoked response
Face
Inversion effect

ABSTRACT

The face is one of the most important visual stimuli in human life, and inverted faces are known to elicit different brain responses than upright faces. This study analyzed steady-state visual-evoked magnetic fields (SSVEFs) in eleven healthy participants when they viewed upright and inverted geometrical faces presented at 6 Hz. Steady-state visual-evoked responses are useful measurements and have the advantages of robustness and a high signal-to-noise ratio. Spectrum analysis revealed clear responses to both upright and inverted faces at the fundamental stimulation frequency (6 Hz) and harmonics, i.e. SSVEFs. No significant difference was observed in the SSVEF amplitude at 6 Hz between upright and inverted faces, which was different from the transient visual-evoked response, N170. On the other hand, SSVEFs were delayed with the inverted face in the right temporal area, which was similar to N170 and the results of previous steady-state visual-evoked potentials studies. These results suggest that different mechanisms underlie the larger amplitude and delayed latency observed with face inversion, though further studies are needed to fully elucidate these mechanisms. Our study revealed that SSVEFs, which have practical advantages for measurements, could provide novel findings in human face processing.

1. Introduction

Face perception has been considered as one of the most important factors of daily life in humans, and previous studies have suggested that processing human faces induces specialized brain responses. Studies using event-related potentials (ERPs) showed that a human face elicited a transient brain response (N170), a posterior negativity peaking approximately 170 ms after face presentation [1–4]. N170 and its corresponding response on magnetoencephalography (MEG), M170, are known to be affected by face inversion. An inverted face elicits delayed [1,5] or delayed and enhanced [6–8] N170, and delayed M170 at least in the right occipito-temporal area [5,9,10]. This effect has been suggested to be face-specific [6], and is referred to as the face inversion effect.

However, face inversion does not appear to induce the same effect in the steady-state visual-evoked response, i.e. the response to a repeatedly presented visual stimulus at a specific frequency [11]. Previous studies reported that steady-state visual-evoked potentials (SSVEPs) were affected by face inversion. Rossion et al. [12] presented upright and inverted face stimuli at 4 Hz and found that both upright and inverted faces elicited SSVEPs in the right occipito-temporal areas at a fundamental frequency of 4 Hz, and that the phase of the SSVEP was delayed for inverted faces, similar to the inversion effect for N170. In contrast, face orientation had no effect on the amplitude of the fundamental frequency response when identical faces were presented repeatedly. Similar results were also found in their other study in which the presentation rate was 3.5 Hz [13]. Gruss et al. [14] demonstrated that the larger SSVEP

---

* Corresponding author. Tel.: +81 564 55 7752; fax: +81 564 52 7913.
E-mail addresses: aki.tsuruhara@gmail.com (A. Tsuruhara), inui@nips.ac.jp (K. Inui), kakigi@nips.ac.jp (R. Kakigi).

0304-3940/$ – see front matter © 2014 Elsevier Ireland Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.neulet.2014.01.001

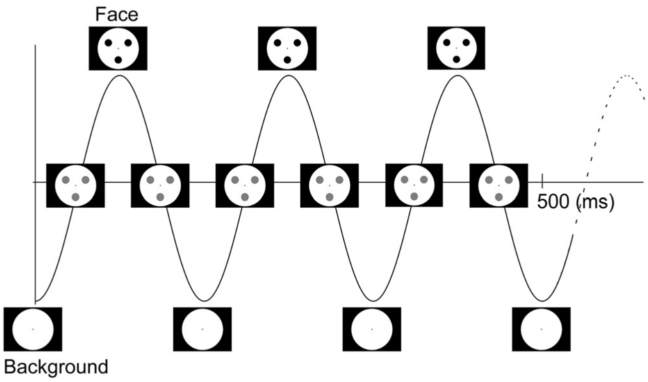

Fig. 1. The Face stimulus and stimulation sequence. The luminance of the stimuli (the three elements in the white background circle) was sinusoidally changed at a rate of 6 Hz so that the lower contrast face stimulus in the midline, in between the background and the full face stimulus, appeared at an intermediary stage of stimulation. The background and fixation circles were kept unchanged during each 8.67-s stimulation sequence.

amplitude with face inversion was absent at low presentation rates (5 and 10 Hz), but was present at higher rates (15 and 20 Hz).

This study analyzed steady-state visual-evoked magnetic fields (SSVEFs) when upright and inverted geometrical faces were presented. Although previous studies examined the face inversion effect on SSVEP as above, its effects on SSVEFs remain unknown. Measuring steady-state responses was shown to have practical advantages such as a high signal-to-noise ratio and shorter experimental time with frequency analyses [e.g. 12]. SSVEFs, as well as SSVEPs, are known to be useful for exploring visual processing [15,16]. The results of the present study may provide clear evidence that the face inversion effect is similar between SSVEF and SSVEP, and that face processing can be examined by measuring SSVEF.

2. Methods

2.1. Participants

Eleven healthy adult volunteers (four females and seven males), aged between 25 and 49 years (mean 35.2; *SD* 6.4), participated in the present study. All participants had normal or corrected-to-normal visual acuity. This study was approved in advance by the Ethics Committee of authors' affiliation, and all participants gave informed consent.

2.2. Stimuli

Stimuli consisted of a face-like geometrical figure (Face), as shown in Fig. 1, and its inversion (iFace). The face inversion effect on N170 was observed with a simple geometrical face-like figure [8]. Thus, a geometrical figure was presented in this study, to avoid any effect of race, gender, attractiveness, or any other factors that could be found in real photographs. All participants reported that they perceived the upright stimulus as a face, and considered the inverted stimulus to be the inversion of the upright stimulus. The figure was composed of a large white circle (30.8 cm in diameter, the same hereafter), three black circles (5.4 cm), and a small red fixation circle (0.4 cm).

Visual stimuli were presented by a personal computer (PC, IBM) and video projector (Mirage 2000; CHRISTIE DIGITAL SYSTEM Inc, Kitchener, Canada) placed outside the magnetically-shielded room, and projected on a screen placed 200 cm from the participant. The refresh rate of the projector was 60 Hz. The projected area was subtended 44.2 cm × 32.9 cm. The luminance of the black circles and the black background was 0.14 cd/m^2, of the large white circle was 2.82 cd/m^2, and of the fixation circle was 0.47 cd/m^2.

The stimulation was given with repeating sessions including two stimulus sequences. In a sequence, one of the two stimuli (Face/iFace) appeared and disappeared 52 times on the screen at a rate of 6 Hz (one face every 166.7 ms). One sequence lasted 8.67 s and followed by another sequence with another type of the stimulus, after a 10-s rest. Epochs with MEG signals larger than 2.7 pT/cm were rejected, and a session, i.e. two sequences, was repeated until four sessions were completed without data rejection for each participant. A 30-s or longer rest was inserted every two sessions. The order of the two sequences (Face/iFace) was randomized in each session and across participants.

The stimulation frequency was determined as 6 Hz for the following reasons. First of all, we wanted to avoid the contamination of noise at the alpha range (8–12 Hz) at the fundamental frequency. The projector refresh rate (60 Hz) was also considered because the stimulus was presented as a sinusoidal (rather than abrupt, as in a square wave function; see Fig. 1) function, consistent with in previous SSVEP studies [12,13,17]. In addition, a recent study demonstrated that a frequency rate of 6 Hz gave the largest SSVEP response to faces [17].

The experiment was conducted in a quiet, magnetically-shielded, and darkened room. Participants passively viewed the display and were asked to maintain their gaze at the fixation circle throughout the experiment.

2.3. MEG recordings

Magnetic signals were recorded using a 306-channel whole-head type MEG system (Vector-view, ELEKTA Neuromag, Helsinki, Finland), which comprised 102 identical triple sensor elements. Each sensor element consisted of two orthogonal planar gradiometers and one magnetometer coupled to a multi-superconducting quantum interference device (SQUID), which provided three independent measurements of the magnetic fields. Signals were recorded with a band-pass filter of 0.1–200 Hz and digitized at 1004 Hz. To record the timing of the stimulus presentation, a trigger was sent from the parallel port of the stimulation computer to the MEG recording.

2.4. Data analysis

We analyzed MEG signals recorded from 204 planar-type gradiometers. These planar gradiometers were powerful enough to detect the largest signal just over local cerebral sources.

To examine SSVEFs, we conducted spectrum analysis on MEG signals and computed the amplitude spectrum as follows. First, a Fast Fourier Transform (FFT) algorithm was applied to an 8159-ms (8192 sampled data) window in each stimulation sequence, for the MEG waveform of each sensor for sequence. To avoid contamination from the transient responses triggered by the onset of the stimulation sequence, the initial 333-ms (2 cycles) waveforms were not included in the spectrum analysis. The frequency resolution was 0.12 Hz (dividing the sampling rate, 1004 Hz, by the sampled data, 8192).

The amplitude and phase of each frequency was then averaged across sequences for Face and iFace. The signal-to-noise ratio (SNR) of the amplitude at each sensor was then computed. The SNR was the ratio of the amplitude at the frequency of interest to the average amplitude of 20 neighboring bins [12,13,18]. The SNR at the fundamental frequency (6 Hz) was extracted for further analyses.

To compare the effect of face orientation on SSVEFs across the visual areas, we selected representative sensors in each visual area (bilateral temporal and occipital areas) as follows. First, sensors