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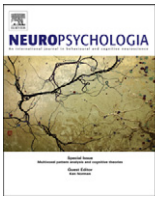

Reversal of the face-inversion effect in N170 under unconscious visual processing

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ABSTRACT

Many studies using electroencephalography consistently reported a larger N170 (N1) response in the visual cortices to inverted than upright face images (the face inversion effect in N1, FIE-N1). Here we report this robust effect is diminished and even reversed when face stimuli are processed unconsciously. We measured visual-evoked potentials to neutral faces either visible or rendered invisible by an inter-ocular suppression. In visible condition, we observed a larger N1 to inverted than upright faces, which replicated the traditional FIE-N1. When those faces became invisible, however, neural responses to the inverted faces were greatly reduced compared to visible condition, whereas those to the invisible upright faces were relatively preserved. Consequently, N1 amplitudes were found to be larger in upright, rather than inverted, faces in invisible condition, which was opposite to the traditional FIE-N1 (upright $<$ inverted) in visible condition. Those results highlighted a special mechanism in the brain for the processing of the upright, but not inverted, face (e.g. fusiform face area) that retains vigorous responses even when the face becomes invisible.

1. Introduction

An inversion of a face image of someone substantially impairs a precise recognition of that face (Valentine, 1988; Yin, 1969). This is called the face inversion effect (FIE) and considered as a marker for a special processing of upright face stimuli in the brain (Yovel & Kanwisher, 2005). A typical explanation for the FIE is that an upright face is perceived holistically (Farah, Tanaka, & Drain, 1995) such that parts of the face (e.g. eyes, a nose, and a mouth) are processed interactively rather than independently, while an inverted face is not. Presenting the face image upside-down thus disrupts this holistic processing, which results in a deteriorated recognition of the inverted compared to upright faces.

Recently, neural mechanisms underlying the FIE have been investigated using neuroimaging techniques, such as functional magnetic resonance imaging (fMRI), electroencephalography (EEG), and magnetoencephalography (MEG). In fMRI, a main focus of those studies was an activity in the face-selective regions in the ventral pathway (Kanwisher, McDermott, & Chun, 1997; Yovel & Kanwisher, 2005), such as the occipital face area (OFA) and fusiform face area (FFA). By comparing hemodynamic responses to upright and inverted faces, previous fMRI studies reported that presenting the inverted face induced comparable or weaker activity in those face-selective regions than the upright face (Aguirre, Singh, & D'Esposito, 1999; Haxby et al., 1999; Yovel & Kanwisher, 2005), suggesting that the inversion of face images disrupts an efficient processing of those images in the OFA and FFA. They also found that a perception of the inverted face elicited a greater activity in the ventral extrastriate regions that respond preferentially to other categories of objects (e.g. houses). Those results indicate that the disruption of holistic processing with the inverted face leads to activation of additional regions in the brain, recruiting not only the OFA and FFA but also other regions for the processing of non-face objects.

While the fMRI studies above provided detailed information about which areas were activated by upright and inverted faces, the temporal resolution of fMRI is limited because it measures hemodynamic signals in the brain. Temporal dynamics of face perception has been investigated by another line of studies using EEG and MEG. In EEG, neural signals from the ventral visual pathway are typically observed as a negative deflection of waveforms measured through electrodes over the occipito-temporal regions, a component known as N170 or N1 (McCarthy, Puce, Belger, & Allison, 1999). Many EEG studies (Anaki, Zion-Golumbic, & Bentin, 2007; Boehm, Dering, & Thierry, 2011; Caharel, Fiori, Bernard, Lalonde, & Rebai, 2006; de Haan, Pascalis, & Johnson, 2002; Eimer, 2000; Itier, Alain, Sedore, & McIntosh, 2007; Jacques & Rossion, 2007; Marzi & Viggiano, 2007; Pesciarelli, Sarlo, & Leo, 2011; Righart & de Gelder, 2006) have consistently reported that, when the face image was presented upside-down, an amplitude of

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the N1 component became larger (FIE-N1). Although the detailed mechanism underlying this FIE-N1 (an enhanced N1 to inverted than upright faces) remains unclear, at least two hypotheses have been proposed that explain this effect (Sadeh & Yovel, 2010). According to the first hypothesis, the FIE-N1 reflects greater effort of the face-selective mechanisms (e.g. OFA and FFA) to process inverted faces, because the inverted faces were more difficult to recognize than upright faces. On the other hand, the second account argues that the FIE-N1 was caused by a recruitment of additional brain regions other than OFA and FFA to process inverted faces. The eye-selective region in the superior temporal sulcus (STS) (Itier et al., 2007) as well as the non-face areas in the extrastriate cortex have been proposed as candidates of those "additional regions".

In the present study, we investigated the FIE-N1 when the face stimuli were rendered invisible through an interocular suppression (Kim & Blake, 2005). A recent study of MEG (Sterzer, Jalkanen, & Rees, 2009) reported that, even though conscious perception of face images was suppressed, those stimuli induced stronger neuromagnetic signals compared to invisible house images, which replicated category-specific responses of N1 (or M170 in MEG) observed in visible stimuli (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Liu, Harris, & Kanwisher, 2002). On the other hand, studies in another group used neutral, fearful, as well as scrambled faces and reported different patterns of neural activity depending on whether those faces were presented in visible or invisible conditions (Jiang & He, 2006; Jiang et al., 2009). We therefore asked presently whether the FIE-N1 to visible face (upright $<$ inverted) was also seen in invisible condition. If any difference in FIE is observed between the two conditions, those results further reveal a unique aspect of unconscious processing of face stimuli and might shed light on neural mechanisms underlying the FIE.

2. Methods

2.1. Subjects

We conducted four experiments in the present study, Experiments 1a, 1b 1c and 2. Ten subjects (eight males, age: 21–31) participated in a main experiment (Experiment 1a), while seven (seven males) out of the ten subjects also participated in the other experiments (Experiment 1b, 1c and 2). They have normal or corrected-to-normal vision. Informed consent was received from each subject after the nature of the study had been explained. Approval for the experiment was obtained from the ethics committee of Kobe University, Japan.

2.2. Experiment 1a

All visual stimuli were generated using Matlab Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) implemented in a PC (DELL OPTIPLEX360), and were presented on a screen of a CRT monitor (SONY MultiScan 17sfII) at a refresh rate of 60 Hz. For dichoptic viewing, we presented stimuli at two different locations on the screen. A square area (delineated by white lines, $6.1 \times 6.1^{\circ}$) on the left half of the screen comprised stimuli for left eyes of the subjects, while another area on the right half comprised those for right eyes. The stimuli at those two locations were fused using a mirror stereoscope placed in front of the subjects' eyes.

We presented subjects with face stimuli unconsciously using continuous flash suppression (CFS) (Tsuchiya & Koch, 2005). In CFS, a rapid sequence of flashes presented to one eye of subjects renders a target image (e.g. face) to the other eye invisible. Every trial in the present study began with a fixation of 1 s (pre-flash period), followed by a rapid sequence of colored Mondrian patterns to a dominant eye of the subject (Fig. 1A). We determined each subject's eye dominance using a variation of the Porta test (Roth, Lora, & Heilman, 2002). In this test, subjects extended one arm and aligned a forefinger vertically with a target object in the room, with both eyes open. Next, they alternately closed each eye, and the dominant eye was defined as the eye that caused a larger alignment change between the forefinger and target object when closed. The duration of each colored pattern was 50 ms, and 26 different patterns were presented in one trial (flash period, 1.3 s). The stimuli to a non-dominant eye, in contrast, were different depending on six types of trials randomly intermixed (Fig. 1B). In high-upright trials, a neutral face image (randomly selected from the faces of six persons, three males and three females) with a high luminance contrast (mean luminance: 19.6 cd/m^2, mean RMS contrast: 11.1 cd/m^2) was presented for 500 ms. Those face images were taken from ATR facial expression image database (DB99, ATR promotions, Kyoto, Japan). The same set of face images was presented in the second condition, being rotated by 180° (high-inverted trials). Because of the high luminance contrast of those images, subjects consciously perceived the upright and inverted faces even during continuous flashes. In the third (low-upright) and fourth (low-inverted) types of trials, on the other hand, the luminance contrast of those face images was lowered (mean luminance: 7.5 cd/m^2, mean RMS contrast: 1.5 cd/m^2) so that subjects could not perceive those faces consciously under CFS. The last two types of trials served as control conditions. In the first type of the control condition (gray trials), we presented no images throughout the flash period, while a static random pattern of visual noise (mean luminance: 7.8 cd/m^2, mean RMS contrast: 3.9 cd/m^2) instead of the face image was given in another type of the control condition (random trials). Those random images were created by the two-dimensional (2D) Fourier transformation of face images (Liu et al., 2002), and thus contained the same spectrums of spatial frequencies as those in the low-upright and -inverted conditions. All images to the non-dominant eye were presented from 600 to 1100 ms after an onset of the continuous flashes (Fig. 1A), so that neural responses to the face images were not confounded with those induced by the onset of continuous flashes. To prevent subjects from perceiving afterimages of the faces or random patterns, we presented continuous flashes also to the non-dominant eye in the last 200 ms of every trial (Sterzer et al., 2009).

At the end of each trial, subjects were asked to perform two tasks sequentially. In the first task, they answered whether the face image was presented during continuous flashes (detection task). They had to press one key when any types of face images (high- or low-contrast, upright or inverted) were detected and another key when not. In the second task, they judged a direction of the face (upright or inverted) with another set of keys. This question was given even if they had answered 'no' in the first task, to check a possibility for the unconscious (subliminal) processing of 'invisible' stimuli. One experimental session consisted of 72 trials in which the six conditions (12 trials for each) were randomly intermixed. Each subject performed six sessions per experiment.

2.3. EEG measurement and data analyses

We recorded EEG signals from 19 points (FP1, FP2, F3, Fz, F4, F7, F8, C3, Cz, C4, T3, T4, T5, T6, P3, Pz, P4, O1, and O2) over the scalp of subjects (EEG1200, NihonKoden, Tokyo, Japan). Those signals were sampled at 500 Hz, and referenced with an average potential measured from right and left ear lobes. Neural activities in response to the face images were investigated by recording visual-evoked potential (VEPs) time-locked to the onset of those images. For each of the 6 conditions above, EEG waveforms in 72 trials at maximum were averaged. An epoch for the averaging ranged from -700 to 500 ms relative to the onset of the face images, with the signals in a period of -50–0 ms used as a baseline.

Although we had assumed that subject could perceive the high-contrast faces presented during the continuous flashes consciously, results in task 1 (detection task) indicated that those high-contrast face were actually invisible in a fraction of trials (see Section 3 and Fig. 1). Likewise, some subjects reported conscious detection of the low-contrast face images during CFS in a small portion of trials. EEG waveforms in those two types of trials were excluded from analyses to ensure a quality of data in the high-contrast (conscious) and low-contrast (unconscious) conditions. Trials in which signal variations were larger than 100 μV were also discarded to prevent a contamination of noise into the data. After the across-trial averaging, a band-pass filter of 0.5–30 Hz was applied to those VEPs. Finally, we examined the face inversion effect by calculating mean VEP amplitudes within specific time windows. To directly compare the FIE between the high- and low-contrast conditions, we used the same time windows for both conditions.

2.4. An objective measurement of visibility: Experiment 1b and 1c

Because an interpretation of the present results crucially depends on whether the low-contrast faces during CFS were truly invisible to subjects, we checked effectiveness of perceptual suppression by performing additional behavioral experiments (Experiment 1b and 1c), using the same set of face images and seven subjects who participated in Experiment 1. In those experiments, we used a two-alternative forced choice (2AFC) task to probe visibility of face images under CFS in a criterion-free way. Our procedures entirely conformed to those in previous studies (Jiang et al., 2009; Sterzer et al., 2009). Each trial in Experiment 1b consisted of two successive temporal intervals (1.3 s for each, with a 500-ms blank gap between them). Stimulus sequences in each interval were identical to those during EEG measurements (continuous flashes to one eye and the face or random image to the other, Fig. 1). The point in Experiment 1b was that a face image (either upright or inverted, high-contrast or low-contrast) was presented in the first or the second interval (randomly determined for each trial), while a random pattern of visual noise (made through a 2D–FFT) was given in the other interval. At the end of each trial, subjects pressed one of two keys to indicate whether the face was presented in the first or second interval (task 1, detection). They then answered a direction of the face image (upright or inverted) that was presented in either interval (task 2, discrimination). An experimental session consisted of 60 trials (24 for the low-contrast upright faces, 24 for the low-contrast inverted faces, 6 for the high-contrast upright face, and 6 for the high-contrast inverted faces), and each subject underwent two or three sessions.