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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 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, Experiment 1a, 1b 1c and Experiment2. Ten subjects (8 males, age: 21-31) participated in a main experiment (Exp. 1a), while seven (7 males) out of the ten subjects also participated in the other experiments (Exp. 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 × 6.1˚) 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, 3 males and 3 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 degrees (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 - 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 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 Results 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 (Exp. 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.

Basic structures of Experiment 1c were the same as those of Experiment 1b, except that we contrasted the face stimulus with a blank, not random, image (corresponding to Gray trials in Exp. 1). As Experiment 1b, we presented a face image in one of two intervals randomly determined, although no image was presented to non-dominant eye in the other interval. Subjects answered an interval in which the face was presented (task 1) and a direction of that face (task 2). Other details were identical to Experiment 1b. Each subjects performed two experimental sessions.

*2.5. Experiment 2*

We compared in Experiment 1 the FIE-N1 under conscious and unconscious states of perception. To manipulate visibility of faces, however, we used two sets of face images with different levels of luminance contrast: the high-contrast faces for visible condition and the low-contrast faces for invisible condition. Although optical properties of the upright and inverted faces were identical within each condition, one might argue that the difference in luminance of stimuli across conditions could hamper a direct comparison of the FIE-N1 between conscious (high-contrast) and unconscious (low-contrast) conditions. To resolve this issue, we created a new visible condition in Experiment 2 using the low-contrast faces in a prior experiment. In this condition, low-contrast face images were presented to non-dominant eye, while a blank grey screen was continuously presented to dominant eye (Sterzer et al., 2009). Because of this lack of continuous flashes to dominant eye, the low-contrast faces to non-dominant eye gained perceptual dominance despite their low luminance contrast, enabling the visible condition using the low-contrast faces.

In each trial of Experiment 2, a low-contrast upright or inverted face was presented to non-dominant eye, and subjects answered a direction of that face (upright or inverted). An experimental session comprising 72 trials (36 for upright and 36 for inverted faces) were repeated twice. Other details were identical to Experiment 1.

## 3. Results

### *3.1. Behavioral data*

**Figure 1B** shows behavioral results of the task 1 (detection task) during EEG measurements (Exp. 1a). Mean (± SE across subjects) detection rates for the high-contrast face images were 98.6 ± 0.9 % (high-upright) and 97.1 ± 2.1 % (high-inverted), indicating that subjects could detect those high-contrast faces even during CFS. In contrast, detection rates for the low-contrast face images were much lower (low-upright: 4.3 ± 2.3 %, low-inverted: 5.4 ±2.9 %), comparable to false alarm rates in the two control conditions (gray: 0.7 ± 0.4 %. random: 2.8 ± 1.1 %) where no face image was presented. Statistical tests revealed results consistent with this view. One-way ANOVA (with Greenhouse-Geisser correction) across the six conditions indicated a significant main effect ($F = 1083$, $p < .001$), and post-hoc comparisons with the Bonferroni correction showed significant differences (corrected $p < .001$ for all) between high-upright vs. low-upright, high-upright vs. low-inverted, high-upright vs. gray, high-upright vs. random, high-inverted vs. low-upright, high-inverted vs. low-inverted, high-inverted vs. gray, high-inverted vs. random. No differences were observed in any pairs between control (gray and random) and low-contrast (low-upright and low-inverted) conditions, even when no correction for multiple comparison was applied ($p > .11$ for all).

We then checked whether those 'invisible' low-contrast faces were unconsciously processed in the brain, using the discrimination task of a face direction (task 2, upright or inverted, **Fig. 1C**). An accuracy of the high-contrast condition was almost 100 % (98.6 ± 0.7 %), significantly higher ($t(9) = 71.6$, $p < .0001$) than chance-level (50 %). On the other hand, the accuracy in the low-contrast condition was 50.1 ± 1.1 %, not significantly different from chance-level ($t(9) = 0.12$, $p = 0.90$). These results shows that the CFS blocked (or at least greatly suppressed) the conscious perception of the upright and inverted faces in the low-contrast conditions, while presentations of the high-contrast faces broke the CFS and conveyed those faces into consciousness of subjects.

Similar results were observed in 2AFC tasks in Experiment 1b and 1c. **Figure 1D** shows detection rate (task 1) and discrimination rate (task 2). When high-contrast images were presented, those detection and discrimination rates were almost 100 %, regardless of whether faces were upright or inverted. On the other hand, task performances for low-contrast faces were 55.8 ± 3.5 % (task 1: upright), 48.3 ± 3.1 % (task 1: inverted), 54.6 ± 9.8 % (task 2: upright) and 44.0 ± 8.7 % (task 2: inverted). One-group t-tests indicated that none of those was larger than chance level ($p > .14$ for all). Similar results were observed in Experiment 1c in which visibility of gray, instead of random, condition was compared with that of face images. Although detection rates of task 1 were slightly above the chance level (upright: 65.2 ± 5.1 %, $p = .025$, inverted: 65.2 ± 6.1 %, $p = .048$), no significant difference from the chance level was observed in discrimination rates of task 2 (upright: 60.1 ± 8.8 %, $p = .29$, inverted: 40.2 ± 7.6 %, $p = .25$). Those results suggest that conscious perception of faces was strongly inhibited in low-contrast conditions.

*3.2. VEP waveforms*

Neural responses to the face (or random-pattern) images were investigated by recording visual-evoked potential (VEPs) from 19 points over the scalp of subjects. **Figure 2** shows grand-averaged (N =10) VEPs at all 19 electrodes, with waveforms in the six conditions superimposed (high-upright: magenta, high-inverted: cyan, low-upright: red, low-inverted: blue, gray: black, random: green). Since we averaged the waveforms from -700 ms to 500 ms relative to the onset of the faces, the VEPs in the first half (-700 ~ 0 ms) were induced by the presentations of the continuous flashes, while those in the second half (0 ~ 500 ms) mainly reflected neural activities to the faces images. After strong activities elicited by the onset of continuous flash (at -600 ms), one could see distinct responses to the face images (0 ~ 500 ms) in the high-upright and high-inverted conditions (magenta and cyan, respectively). These responses to the face images were characterized by N1 (N170) at posterior channels (O1, O2, T5, T6, P3 and P4, see orange circles in **Fig. 2**). Those N1 responses to the high-contrast faces at posterior electrodes were enlarged in **Figure 3**. At all six channels

(O1, O2, T5, T6, P3 and P4), amplitudes of the N1 components tended to be larger in the high-inverted (cyan) compared to high-upright (magenta) conditions, reflecting the traditional FIE-N1. This tendency was statistically tested below, using the mean VEP amplitudes across the four (high-/low-contrast × upright/inverted) conditions.

In contrast to a clear FIE-N1 in the high-contrast (conscious) conditions, we found that the same effect was totally diminished in the low-contrast (unconscious) conditions (**Fig. 4A**). In those low-contrast conditions, we observed two separate components of VEPs instead of a large single-peaked N1 in the high-contrast conditions. We thus named the first component as N1a (130-170 ms) and second component as N1b (220-260 ms). In both N1a and N1b components, low-upright face images (red in **Fig. 4A**) induced stronger responses than low-inverted faces (blue). To compare the FIE-N1 between visible (high-contrast) and invisible (low-contrast) conditions, we performed a two-way ANOVA of visibility (high-contrast or low-contrast) × orientation (upright or inverted) using mean EEG amplitudes in the four conditions. The two-way ANOVA applied to N1a (**Fig. 4B**) yielded a significant main effect of visibility ($F(1,27) = 16.15$, $p < .001$) and an interaction ($F(1,27) = 12.99$, $p < .001$). Post-hoc analysis revealed significant difference between upright and inverted faces in high-contrast conditions (upright < inverted, $t(9) = 2.44$, $p = .03$). A significant difference in an opposite direction (upright > inverted, $t(9) = -3.46$, $p = .007$) was observed in low-contrast conditions, which showed a reversal of FIE-N1 depending on visibility of faces. The same statistical results were also observed in N1b (**Fig. 4C**). The two-way ANOVA indicated a significant main effect of visibility ($F(1,27) = 55.97$, $p < .001$) and an interaction ($F(1,27) = 8.09$, $p = .008$), with significant differences between upright and inverted faces both in high-contrast (upright < inverted, $t(9) = 3.41$, $p = .008$) and low-contrast conditions (upright > inverted, $t(9) = -5.17$, $p = .0006$).

To directly compare magnitudes of the FIE-N1 between conscious (high-contrast) and unconscious (low-contrast) conditions, we finally made the face inversion index (FII, **Fig. 4D**), using the mean amplitudes of N1a and N1b. This index corresponds to a difference in mean amplitudes between the upright and inverted conditions divided by a sum of those two, as shown in the equation below:

$$FII = (A_{Upright} - A_{Inverted}) / (A_{Upright} + A_{Inverted})$$

where $A_{Upright}$ and $A_{Inverted}$ denote absolute mean amplitudes of N1a (N1b) for the upright and inverted faces, respectively. Positive FIIs should indicate larger N1a (N1b) responses to the upright than inverted faces. In case that mean amplitudes had opposite signs between upright and inverted faces, we performed a correction of those amplitudes by subtracting a fixed value so that all amplitudes of N1a or N1b had a negative value smaller than -1 (Sadeh, Podlipsky, Zhdanov, & Yovel, 2010). After averaging the mean amplitudes across the six channels (O1, O2, P3, P4, T5 and T6), we calculated this FII for each of high-contrast and low-contrast conditions. As shown in **Figure 4D**, those FII were negative for high-contrast and positive for low-contrast condition. A t-test revealed significant difference in FII between high-contrast and low-contrast conditions in both N1a ($t(9) = 4.76$, $p = .001$) and N1b ($t(9) = 6.17$, $p = .0002$). Those results demonstrated the reversed FIE-N1 in unconscious face processing that were broadly observed in posterior regions in the brain.

### *3.3. Supplementary analyses of EEG data using seven subjects*

Although ten subjects participated in Experiment 1a, seven out of the ten subjects took part in Experiments 1b and 1c. This inhomogeneity of subject groups might prevent comparison of results across experiments. We therefore reanalyzed the EEG data in Experiment 1a using the data of the seven subjects who participated in the other experiments.

The results were shown in **Figure 5**. The two-way ANOVA applied to N1a (**Fig. 5A**) yielded a significant main effect of visibility ($F(1,18) = 7.64$, $p = .013$) and an interaction ($F(1,18) = 14.95$, $p = .001$). Post-hoc analysis revealed significant difference between upright and inverted faces in high-contrast conditions (upright < inverted, $t(6) = 5.31$, $p = .002$). A marginally significant difference in an opposite direction (upright > inverted, $t(6) = -2.43$, $p = .051$) was observed in low-contrast conditions. The same statistical results were also observed in N1b (**Fig. 5B**). The two-way ANOVA indicated a significant main effect of visibility ($F(1,18) = 94.66$, $p < .001$) and an interaction ($F(1,18) = 19.18$, $p < .001$), with significant differences between upright and inverted faces both in high-contrast (upright < inverted, $t(6) = 7.99$, $p = .0002$) and low-contrast conditions (upright > inverted, $t(6) = -3.81$, $p = .009$). The results of FII also resembled those in a previous analysis using ten subjects (**Fig. 5C**). Significant differences between low-contrast and high-contrast conditions were observed both in N1a ($t(6) = 3.77$. $p = .009$) and N1b ($t(6) = 6.30$. $p = .0007$).

*3.4. Experiment 2*

In Experiment 1 we presented two sets of face images with different luminance contrasts, low-contrast faces for invisible and high-contrast faces for visible conditions. One thus might argue that the reversed FIE-N1 did not reflect difference in neural processing of visible and invisible stimuli but result from lowered luminance of stimuli in invisible condition. To resolve this issue, we measured in Experiment 2 VEPs to the low-contrast faces without CFS. If the reversed FIE-N1 was caused by low luminance contrast of faces, it should be also observed in this experiment.

The results of Experiment 2 were shown in **Figure.6**. At all six channels, larger N1 amplitudes were induced by inverted face than upright face (**Fig.6A**). Negative peak amplitudes in a typical time window of N1 (140-220 ms) showed a significant difference between upright and inverted conditions ($t$(6) = 2.68, $p$ = .04, **Fig.6B**). These results replicated the traditional FIE-N1, and thus indicate that the reversal of FIE-N1 in Experiment 1 was not caused by the lowered contrast of images but represented the difference in neural mechanisms between conscious and unconscious processing.

## 4. Discussion

In this experiment, we recorded VEPs to face stimuli consciously or unconsciously processed during CFS. When high-contrast face images were presented, these images broke the suppression and entered consciousness of subjects (**Fig. 1**). The conscious perception of faces induced clear N1 components of EEG at posterior electrodes, which showed stronger responses for the inverted than upright faces (FIE-N1, **Fig. 3**). In contrast, low-contrast face images presented during CFS were kept invisible, as shown in the low detection and discrimination rates of the two tasks (**Fig. 1**). Nevertheless, those low-contrast faces elicited significant negative deflections of EEG waveforms at the posterior positions (**Fig. 4**), reflecting unconscious neural responses to invisible face images (Fang & He, 2005; Jiang & He, 2006). We found that those neural responses were stronger to invisible upright than inverted faces, resulting in the reversed FIE-N1 (upright > inverted) in unconscious neural processing.

### *4.1. Neural mechanisms underlying the reversed FIE-N1.*

Why was the FIE-N1 reversed in unconscious processing? As is seen in **Figure 4**, this reversal was mainly caused by the N1 to upright faces that maintained vigorous responses even in invisible (low-contrast) condition. In N1a, for example, mean amplitudes to inverted faces were -2.6 μV in visible (high-contrast) and -0.6 μV in invisible conditions, which indicates that a suppression of conscious perception by CFS reduced EEG responses to inverted faces by about 80 %. In contrast, the N1a to invisible upright faces (-1.6 μV) was relatively preserved compared to visible condition (-1.7 μV). Although the N1 amplitudes were higher to inverted than upright faces in visible condition (normal FIE-N1), this difference in reduction rates under CFS produced higher N1 responses to upright than inverted faces in invisible condition, resulting in the reversed FIE-N1.

We presume that the preserved N1 responses to invisible upright face are related to the highly-specialized mechanisms in the brain for the processing of upright faces. Many electrophysiological studies using monkeys reported neurons in the ventral pathway that showed strong activity to upright faces (Perrett et al., 1985; Tsao, Freiwald, Tootell, & Livingstone, 2006). Previous fMRI studies also reported somewhat higher responses of the face-selective regions to upright than inverted faces (Aguirre et al., 1999; Haxby et al., 1999; Yovel & Kanwisher, 2005). Those specialized systems for the processing of upright faces would enhance a sensitivity of the brain to those faces, which enables strong EEG responses even when conscious recognition of face information was hampered by the interocular suppression. In contrast, these specialized systems for upright faces would not work for inverted faces because inverted faces were recognized in the brain as non-face objects rather than faces, as suggested by previous studies (Aguirre et al., 1999; Haxby et al., 1999). This lack of the specialized mechanisms resulted in a great reduction of EEG signals to inverted faces when those faces were rendered invisible by CFS.

Our EEG results go along with previous psychophysical studies investigating the unconscious processing of face stimuli (Jiang, Costello, & He, 2007; Zhou, Zhang, Liu, Yang, & Qu, 2010). In those studies, an upright or inverted face was presented to a subject under CFS. Because a luminance contrast of the face was low at the beginning of a trial, the face was rendered invisible by the continuous flashes to the other eye. The luminance contrast of the face, however, increased gradually over time, breaking suppression and entering consciousness of the subject at a specific time within the trial. They found that the upright faces took less time to gain perceptual dominance compared to the inverted faces. These results suggest a higher sensitivity of the brain to upright than inverted faces unconsciously processed, which is consistent with the preserved N1 responses to invisible upright faces in the present study.

*4.2. Temporal dynamics of EEG signals to faces under CFS*

While we showed a reversal of the FIE-N1 between conscious and unconscious processing of faces, it should be noted that the temporal dynamics of the N1 in the present study differed from that in previous studies in several ways. First, we observed that the present N1 measured during CFS was delayed compared to a typical N1 response without CFS. As shown in **Figure 7A**, peak latency of the N1 to high-contrast faces under CFS was around 210 ms, whereas the latency in Experiment 2 (no CFS) was 170-180 ms. This extension of the N1 latency under CFS was also seen in a previous EEG study (Jiang et al., 2009). Although a reason for this extension is unclear, one possibility would be a lowered excitability of neurons in the visual cortex during CFS (Noguchi, Yokoyama, Suzuki, Kita, & Kakigi, 2012). Since we presented a sequence of colorful Mondrian patterns (continuous flashes) for 600 ms before an onset of face images, those flashes must have strongly activated neurons in the visual cortex, inducing a habituation (a reduction of excitability) of those neurons. This lowered excitability in the visual cortex might delay EEG responses to a subsequent face image, resulting in the extension of the N1 latency under CFS.

Another feature in the present N1 response was two separate components (N1a and N1b) observed in invisible condition. We compared in **Figure 7B** EEG waveforms to high-contrast (visible) and low-contrast (invisible) upright faces in Experiment 1. One could see that the N1a in invisible condition emerged around 100 ms, slightly after an emergence of the N1 in visible condition. On the other hand, both the N1b (in invisible condition) and the N1 (in visible condition) went back to the baseline about 300 ms. Those patterns of EEG waveforms suggest that two separate EEG components might be intermixed within the N1 time range in the present study. Although this mixture of the two components was unclear in visible (high-contrast) condition, weak neural responses to low-contrast faces might make their distinction clear. The first possibility was that N1a corresponded to the N1 (N170) component in visible condition, while the N1b reflected another EEG component, such as N250 that was implicated in detailed analysis of face stimuli (Tanaka & Pierce, 2009). Alternative account is that the N1a and N1b represented neural signal from the OFA and FFA, respectively. Although we could not perform a precise estimation of source locations for the N1a and N1b due to a low spatial resolution of EEG, future studies using MEG or electrocorticography (EcoG) might reveal anatomical and functional distinctions of those two components.

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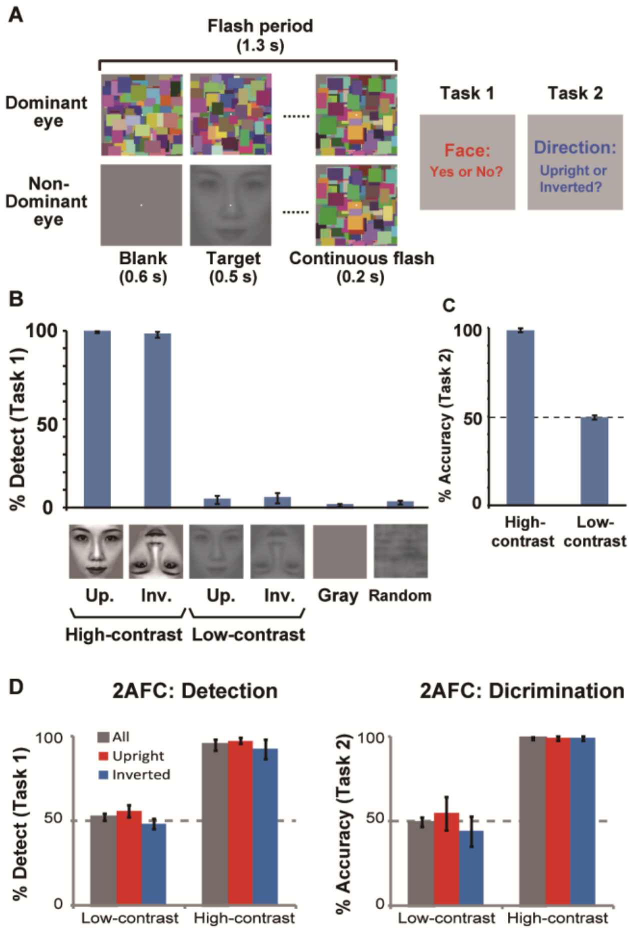


**Figure 1.** Stimuli, tasks, and behavioral results. (**A**) A sequence of one trial and tasks. Two different images were given to dominant and non-dominant eyes of a subject, being fused by a mirror stereoscope. After one second of a fixation screen (not shown), continuous flashes (20 Hz) were presented to the dominant eye, which rendered a target image (e.g. face, see below) to the non-dominant eye invisible (continuous flash suppression or CFS). When the continuous flashes disappeared, subjects performed two tasks (detection and discrimination tasks for the faces presented in subset of trials). (**B**) Six types of images given to the non-dominant eyes and detection rates in task 1. When upright and inverted faces with a high luminance contrast were presented during the continuous flashes, those face broke the suppression and came into consciousness of subjects (left two bars). In contrast, most upright and inverted faces with a low luminance contrast (middle two bars) were kept invisible throughout the end of the trial. As a control, we employed two conditions where no

image was presented (gray trials) and a static random pattern with same spatial spectrum as the low-contrast face was given (random trials). False-alarm rates in those conditions (right two bars) were comparable to the detection rates in the low-contrast conditions (middle two bars). (**C**) Behavioral results in task 2 (a discrimination of face directions). Mean accuracies in the high-contrast and low-contrast condition were 98.6 % and 50.1 %, respectively. No significant difference from the chance level (50 %) was observed in the low-contrast conditions, indicating that the face perception in the low-contrast condition was totally suppressed during the flash period. (**D**) Results in Experiment 1b (a behavioral experiment). Subjects conducted the detection (left) and discrimination (right) tasks again but with a two-alternative forced choice (2AFC) design (see Methods for details). In both tasks, their performances for low-contrast faces were near the chance level (50%), indicating that those faces were kept invisible through the experiment. In this and subsequent figures, all error bars denote standard errors (SEs).

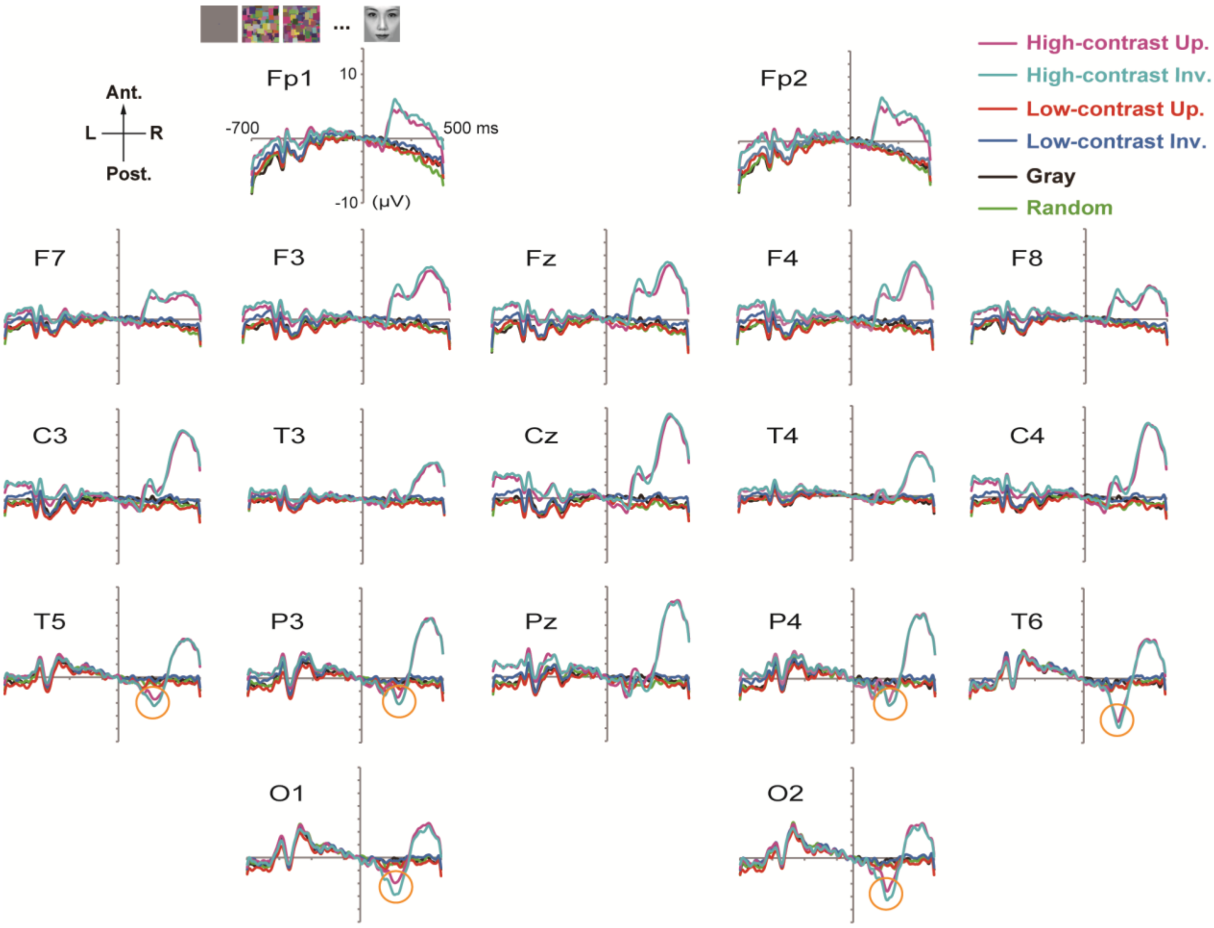


**Figure 2.** Spatial distribution of the N1 (N170) responses. Visual-evoked potentials (VEP, positive: upward) averaged across all ten subjects at 19 electrode positions over the scalp. Waveforms in the six conditions (**Fig. 1B**) were superimposed. Zeros in the horizontal axis indicate an onset of the face images. A left half of each waveform (-700 ~ 0 ms) shows VEP induced by a presentation of continuous flash and a right half (0 ~ 500 ms) represents those mainly elicited by faces or random patterns. Distinct N1 (N170) responses were observed in posterior six channels (P3, P4, T5, T6, O1 and O2, orange circles), especially in the high-upright (magenta) and -inverted (cyan) conditions where subjects recognized the face images consciously. Those N1 components were followed by positive responses (P2) in anterior electrodes.

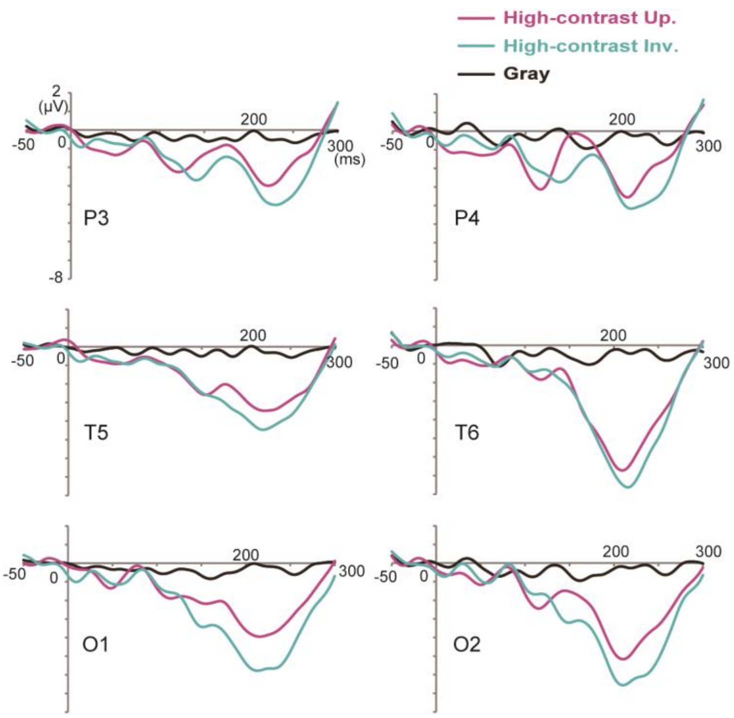


**Figure 3.** EEG responses to the high-contrast face images. VEPs to the high-contrast faces at -50 ~ 300 ms after an onset of stimuli (faces). Waveforms in the high-upright (magenta) and –inverted (cyan) conditions as well as the control condition (black) were plotted at each six posterior electrodes (P3, P4, T5, T6, O1 and O2).

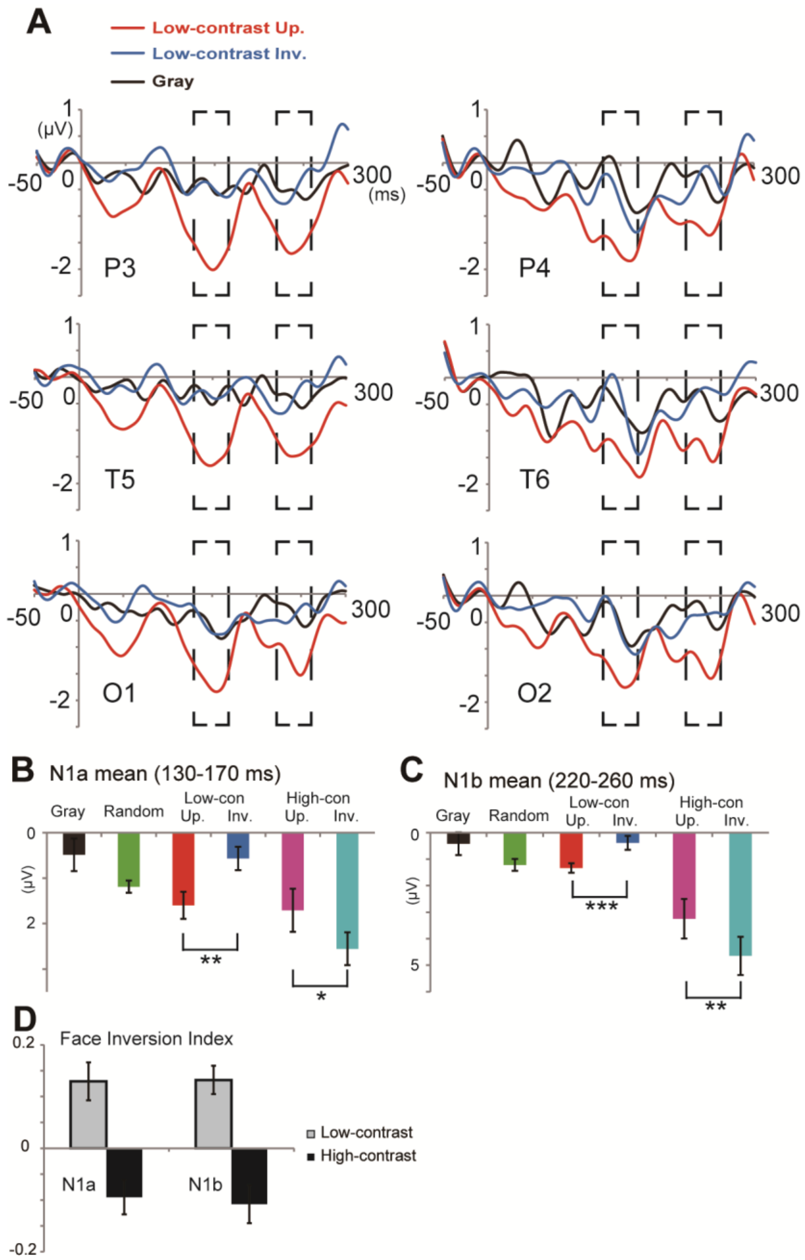


**Figure 4.** EEG responses to the low-contrast face images. (**A**) VEPs to the low-contrast faces at -50 ~ 300 ms after an onset of stimuli (faces). Waveforms in the low-upright (red) and -inverted (blue) conditions as well as the control condition (black) were plotted at each of six posterior electrodes (P3, P4, T5, T6, O1 and O2) where the N1 responses were evident in high-contrast conditions (**Fig. 2A**). (**B**) A comparison of N1a responses in all six conditions. For each subject, mean ERP amplitudes from 130 to 170 ms (dotted left rectangles in **A**) were averaged across the six channels. Error bars denoted SE across the ten subjects. In high-contrast conditions, inverted faces induced a stronger N1 response than upright faces,

replicating the normal face inversion effect in N1 (FIE-N1, upright < inverted) reported by previous EEG studies. This FIE-N1 was, however, reversed in low-contrast conditions (upright > inverted). (**C**) A comparison of N1b responses in all six conditions. We analyzed mean ERP amplitudes in a time window of 220 to 260 ms (dotted right rectangles in **A**). The results in N1b were similar to those of N1a. (**D**) Face Inversion Index. The FII shows a difference in the N1a (or N1b) amplitudes between upright and inverted conditions (upright - inverted) divided by a sum of those two (see Results for details). If the normal FIE-N1 (upright < inverted) arises, this index should be negative. In both N1a and N1b, the FIIs were negative in the high-contrast (conscious) condition (black bars), while those were positive in the low-contrast (unconscious) condition (gray bars).

* $p < .05$, ** $p < .01$, *** $p < .001$.

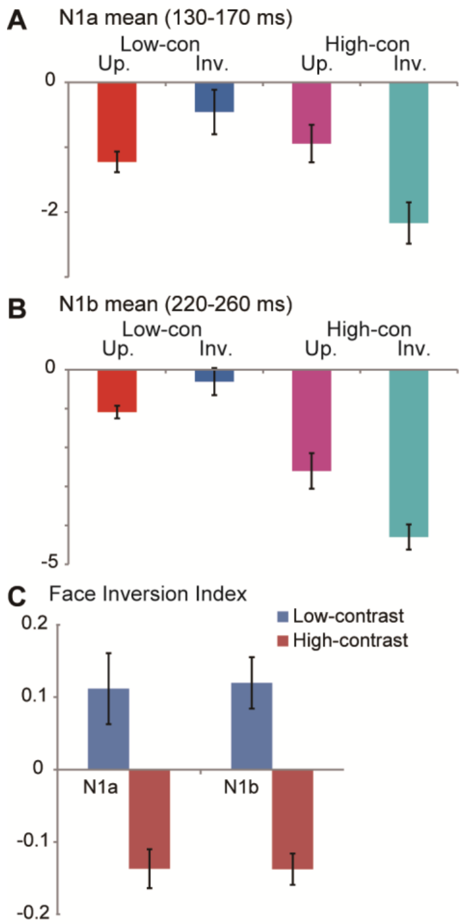


**Figure 5.** Supplementary analyses of N1a and N1b using seven subjects participating in the other experiments (Exp.1b and 1c). (**A**) A comparison of mean N1a responses in low-contrast and high-contrast conditions. (**B**) A comparison of mean N1b responses in low-contrast and high-contrast conditions. (**C**) FIIs. Our main results (a reversal of FIE-N1 between visible and invisible conditions) were unchanged even when a group of subjects was matched. Error bars denoted SE across the seven subjects.

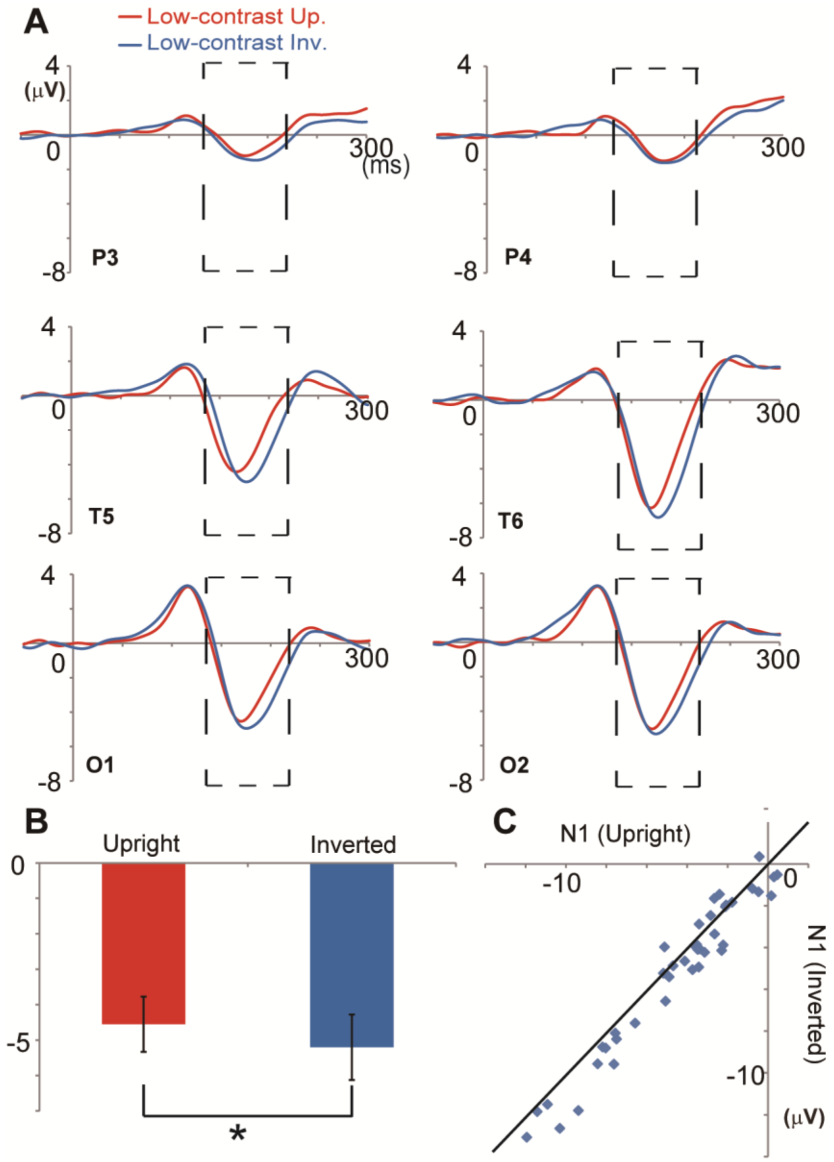


**Figure 6.** Results of Experiment 2 (neural responses for low-contrast faces under no-CFS). (**A**) VEPs to the low-contrast faces at -50 ~ 300 ms after stimuli onset at all six channels. Waveforms in the low-upright (red) and low-inverted (blue) were plotted. (**B**) Mean amplitudes of N1 (140-220 ms). (**C**) A one-by-one plotting of N1 amplitudes between upright (abscissa) and inverted (ordinate) conditions. Each point represents mean N1 amplitude for one of the six channels in each subject. Both a bar graph (**B**) and a scatter plot (**C**) show larger N1 responses to inverted faces, replicating the traditional FIE-N1. * $p < .05$.

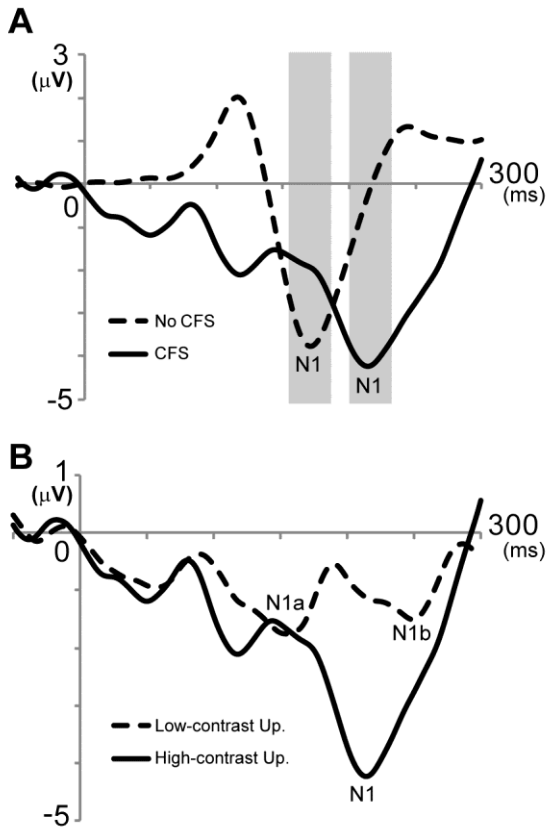


**Figure 7.** N1 responses in conscious and unconscious conditions. (**A**) The neural responses to upright faces presented during CFS (solid line, the high-contrast condition in Exp.1a) and under no-CFS (dotted line, Exp.2). Waveforms in the six channels were averaged. Although the N1 response with a typical latency (170 – 180 ms) was observed in no-CFS condition, the latency of the same component in CFS condition was delayed about 30 - 40 ms. (**B**) N1 responses for high-contrast (conscious) and low-contrast (unconscious) conditions in Exp.1a. A neural response to high-contrast upright faces (solid line) and low-contrast upright faces (dotted line). In the low-contrast condition, first peak is called N1a (130 – 170 ms) and second peak is called N1b (220 - 240 ms). While two separate N1 components (N1a and N1b) were seen in the low-contrast condition, one could see that an onset of N1a was synchronized with that of N1 in conscious condition. An offset of N1b was also synchronized with that of N1, which indicates that a suppression of conscious perception of faces reduced the N1 amplitudes, resulting in a separation of N1a and N1b.